EXAMINING MECHANISMS CONTRIBUTING TO THE BIOLOGICAL VARIATION OF RESIDUAL FEED INTAKE IN GROWING HEIFERS AND BULLS AND IN MID-GESTATION FEMALES

A Dissertation

by

AIMEE NICOLE HAFLA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2012

Major Subject: Animal Science

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Approved by:

Chair of Committee,	Gordon D. Carstens
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ABSTRACT

Examining Mechanisms Contributing to the Biological Variation of Residual Feed Intake in Growing Heifers and Bulls and in Mid-Gestation Females. (August 2012)

Aimee Nicole Hafla, B.S., Montana State University;

M.S., Montana State University

Chair of Advisory Committee: Dr. Gordon E. Carstens

The objectives of this study were to characterize residual feed intake (RFI) in growing bulls and heifers and in mid-gestation females to examine relationships with performance, body composition, feeding behavior, digestibility (DMD) and heart rate (HR) and evaluate the impact of RFI on bull fertility and cow forage utilization. Additionally, use of the n-alkane method to predict individual animal variations in intake was investigated. To accomplish these objectives, multiple RFI studies were conducted. In all studies RFI was computed as the difference between actual and expected DMI from linear regression of DMI on mid-test metabolic BW and ADG.

To evaluate phenotypic relationships between feed efficiency, scrotal circumference (SC) and semen-quality an experiment was conducted with yearling bulls (N=204). Residual feed intake was not correlated with BW and ADG, but was positively associated with 12th-rib back fat (BF) such that the more efficient bulls were leaner. Bulls with low RFI had similar SC and progressive motility of sperm compared to high-

RFI bulls. However percent normal sperm were weakly associated with RFI in a negative manner.

To examine phenotypic relationships between heifer postweaning RFI, and performance, efficiency, HR, and DMD of mid-gestation cows, RFI was measured in growing Bonsmara heifers (N=175). Forty-eight heifers with divergent RFI were retained for breeding. Subsequently, intake, performance and feeding behavior was measured on mid-gestation females. Pregnant females classified as having low postweaning RFI continued to consume 22% less feed, spent 25% less time eating, and had 7% lower HR while maintaining similar BW, ADG and body composition compared to high RFI females. A moderate association between RFI in growing heifers and subsequent efficiency of forage utilization in pregnant cows was found. Growing heifers identified as efficient had greater DMD, however DMD in mature cows was similar between RFI groups. The n-alkane method of predicting intake detected differences in intake between divergent RFI groups in mid-gestation females.

Results from this study indicate that inclusion of RFI as a component of a multi-trait selection program will improve feed efficiency of growing animals and mid-gestation females with minimal impacts on growth, body composition, and fertility traits.

DEDICATION

This dissertation is dedicated to my mother, Linda Hafla. From my first science fair to my graduation from Texas A&M University, it was your constant support and encouragement that made this possible.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

Global prices for major food commodities have reached historical highs in recent years (USDA-ERS, 2012) reflecting rapidly increasing commodity prices induced in part by global demand for food that many experts project will likely double and maybe even triple, over the next 50 years. With increasing input costs, agricultural researchers and producers are faced with the task to identify, develop and adopt technologies that will enable more efficient and sustainable production of food and fiber.

Feed is the single largest variable expense associated with the production of beef, and accounts for approximately 65% of total expenses required to maintain a breeding herd (Arthur et al., 2004; Van der Westhuizen et al., 2004). The USDA Agricultural Census reported that the steepest increase in the costs of producing beef was that associated with feed, which increased 45% from 2002 to 2007. As more than two-thirds of total feed inputs needed for the production of beef are required by the cow-calf sector, breeding programs that identify cows that have lower maintenance energy requirements and improved feed utilization would greatly reduce costs of beef production systems. Ratio-based traits such as gain to feed (G:F) have been the traditional measure of feed

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This dissertation follows the style of Journal of Animal Science.

efficiency. However, due to strong genetic associations with growth, favorable selection for G:F will result in a greater mature cow size, and subsequently greater maintenance energy requirements for the cow herd (Herd and Bishop, 2000). Residual feed intake (RFI) provides a measure of feed efficiency that is independent of growth traits (Herd and Arthur, 2009) and is moderately heritable (Herd et al., 2003).

The concept of RFI was first introduced by Koch et al. (1963) as the difference between actual intake and expected feed intake based on body size and growth. Animals that consume less feed than expected are considered to be efficient (low RFI), and those that consume more feed than expected are considered inefficient (high RFI). Residual feed intake is calculated by a linear regression of DMI on ADG and metabolic BW ($MBW^{0.75}$):

$$y = \beta_0 + \beta1(ADG) + \beta2(MBW) + RFI$$

where y is DMI, β0 is the regression intercept, β1 is the partial regression of daily intake on ADG, and β2 is the partial regression of daily intake on BW expressed as metabolic BW (MBW).

The use of linear regression forces RFI to be independent of the component traits (BW and ADG) used in the computation of expected DMI. Therefore, RFI is a feed efficiency trait that accounts for inter-animal variance in feed intake that is not explained by variations in BW and ADG. Previous studies have reported RFI to be moderately heritable (0.35 to 0.40) (Arthur et al 2001a,b; Schenkel et al., 2004; Nkrumah et al., 2004, 2007). Progeny from parents resulting from 1.5 generations of selection for low RFI have been found to consume 11.3% less feed, but were similar in yearling BW and

ADG, indicating that selection for improved RFI will facilitate improvements in production efficiency of subsequent generations (Arthur et al., 2001c). To make selection of efficient cattle cost-effective, it is imperative to understand the physiological and genetic factors that contribute to variation in feed efficiency and examine associations between RFI and other economically relevant traits (e.g., fertility, carcass quality).

Biological Sources of Variation in Residual Feed Intake

Richardson and Herd (2004) summarized the biological basis for phenotypic variation in RFI in beef cattle (Figure 1.1) and indicated that digestion accounted for 10% of the biological variation, activity for 10%, heat increment for 10%, body composition for 5%, feeding patterns for 2% protein turnover, tissue metabolism and stress for 37%, and finally 27% for other processes.

Genetic variations in maintenance energy requirements are closely associated with energetic variations in RFI in beef cattle (Herd and Bishop, 2000). Feed energy for maintenance represents between 60 and 75% of the total individual energy requirements of the breeding animal (Archer et al., 1999). Brosh et al. (1998) investigated the use of heart rate to estimate energy expenditure in cattle. The authors reported that average heart rate and daily energy expenditure in Hereford heifers on low energy diets were less than values for animals on high energy diets. Moreover, the authors noted that the convenient measure of heart rate was an accurate method to estimate energy expenditure.

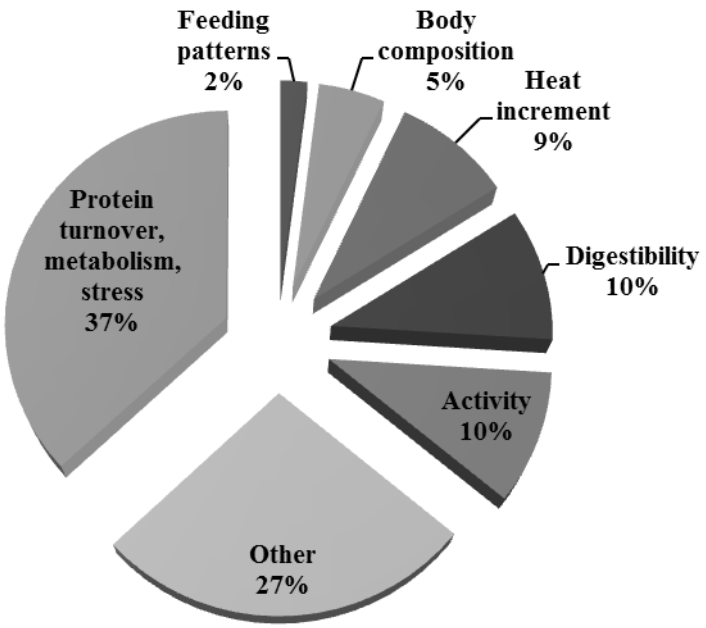

Figure 1.1 Biological contributions to the variation in residual feed intake (Herd and Arthur 2009).

These findings imply that heart rate may serve as an indicator trait for differences in energy expenditure in beef cattle.

Many studies have reported that between-animal variance in body composition contributes to variation in RFI of growing animals (Richardson et al., 2001; Nkrumah et al., 2004; Schenkel et al., 2004; Shaffer et al., 2011; Lancaster et al., 2009a,b; Lawrence et al., 2011; Kelly et al., 2010a,b). Most studies have reported positive genetic and phenotypic associations between RFI and subcutaneous fat depth (Schenkel et al.. 2004; Nkrumah et al., 2007; Lancaster et al., 2009a,b), and the inclusion of backfat thickness in models to compute RFI have typically accounted for an additional 2-4 percentage units variation in DMI beyond that assigned to ADG and MBW (Arthur et al., 2003; Basarab et al., 2003; Lancaster et al., 2009a,b).

Factors that influence digestibility include, but are not limited to level of intake, passage rate, environmental conditions, breed difference, and dietary characteristics (Church, 1988). In ruminants, it is generally accepted that as level of intake increases digestibility decreases, therefore high-RFI cattle that have greater intakes may have lower apparent dry matter digestibility (DMD). Finding evidence of differences in digestibility in beef cattle with divergent RFI have proven difficult; however, weak associations and numeric differences indicating greater digestibilities in low-RFI cattle have been reported (Nkrumah et al., 2006; Krueger et al., 2009; Cruz et al., 2010; McDonald et al., 2010). Richardson et al. (1996) reported the low-RFI steers had 1% greater DM digestibility compared to low-RFI steers, and concluded that small

differences in digestibility may contribute to observed between-animal differences in feed efficiency.

Several studies have evaluated relationships between feeding patterns, intake and feed efficiency in beef cattle (Basarab et al., 2007; Nkrumah et al., 2007; Bingham et al., 2009; Lancaster et al., 2009b; Kelly et al., 2010b). Kelly et al. (2010b) reported positive associations between RFI and bunk visit frequency, visits to the bunk without consuming feed, and eating rate in growing beef heifers. In agreement, Montanholi et al. (2009) found positive correlations between feed efficiency and bunk visit duration, bunk visit frequency, eating rate, and meal size in growing steers. Lancaster et al. (2009b) also found that RFI was positively correlated with meal duration, head-down duration, and meal frequency, and reported that between-animal variation in these feeding behavior traits accounted for about 35% more variation in DMI than ADG and MBW. These studies indicate that inefficient heifers and steers spend more time eating and likely expend more energy on activities associated with feeding. These relationships suggest that the differences in feeding activities contribute to the variations in RFI because of the energetic costs related to these activities.

Human studies have linked activity to energy expenditure, using accelerometer technology (Levine et al., 2001). Moreover, research has reported that high-RFI mice were 2 to 3 times more active than low RFI mice (Mousel et al., 2001; Bunger et al., 1998). Clark et al. (1972) recognized that cattle expend more energy when standing compared to lying and that to obtain correct measurements of heat production, an adjustment for activity may be useful. Hall and Brody (1933) found a 9% increase in

heat production due to standing over lying with an additional 2.5 kcal per 100 kg live weight, expended for each double body change. Variations of energy expenditures from activity result in differentness of heat production and energy available for maintenance and growth (Herd and Arthur, 2009). Richardson et al. (1999) found a phenotypic correlation of 0.32 for RFI with a daily pedometer count, explaining 10% of the variation in RFI may be contributed to activity. Differences in physical activity may contribute to the variation in energy expenditure between efficient and inefficient animals, and may hold possibilities as an indicator trait.

Many integrated biological mechanisms contribute to variations in RFI (Richardson and Herd 2004; Herd and Arthur, 2009). An understanding of how these mechanisms are associated with differences in feed efficiency is necessary to further understand how selection for this trait may impact other economically relevant traits.

Residual Feed Intake and Bull Fertility

Progressive seedstock producers are adopting technology to measure daily intake to assess feed efficiency of growing bulls and heifers. Inclusion of RFI in selection indexes will enable selection for feed efficiency with minimal effects on growth and other performance traits. However, the impacts of selection for RFI on breeding soundness and bull fertility have not been extensively investigated.

Scrotal circumference (SC) in young bulls has been shown to be moderately correlated with total sperm production and age at puberty in female offspring (Hahn et al., 1969; Lunstra and Echiternkamp, 1982; Gipson et al., 1985). Heritability estimates

for scrotal circumference have been reported to be moderate to high (0.43 to 0.53; Koots et al., 1994; Bourdon and Brinks, 1986) in growing bulls. Fields et al. (1982) reported that age of bull, breed, and environmental factors can affect sperm motility and concentration, and testicular volume, and thus cause variation in fertility of growing bulls. Scrotal circumference is correlated with sperm production and is an important trait when evaluating breeding soundness of young bulls (Hahn et al., 1969; Lunstra and Echternkamp, 1982; Gipson et al., 1985). Arthur et al. (2001a) and Schenkel et al. (2004) found that final SC was phenotypically and genetically independent of RFI in growing bulls. Crews et al. (2006) derived a 3-trait selection index for growing bulls based on RFI, ADG and 365-d yearling BW to predict genetic merit for net revenue of feedlot progeny. The index value was favorably correlated with RFI, DMI and ADG (0.74, -0.22 and 0.53, respectively), but was not correlated with yearling BW, such that high index bulls consumed less DMI, gained faster and had similar yearling BW compared to bulls with low index values. The selection index tended to be positively correlated with SC (0.16), which likely reflects the positive association between SC and ADG. These results suggest that multiple-trait indexes that incorporate RFI would not be expected to result in unfavorable selection for low SC.

Very little research is available in ruminants regarding the impacts of feed efficiency on semen quality traits. Barber and Almquist (1975) reported that, based on a single pubertal ejaculation, Charolais bulls selected for rapid growth had decreased initial sperm motility and decreased live sperm per ejaculate when compared to their slower gaining counterparts. Siegel (1963) and Marini and Goodman (1969) also

indicated that selection for rapid growth was associated with lower percent of normal sperm and lower motility in broilers and bulls. Inadequate body fat has been reported to negatively impact SC, sperm motility and sperm morphology in bulls (Barth and Waldner, 2002), however excess fat has also been associated with decreased sperm production and seminal quality (Mwansa and Makarechian, 1991; Coulter et al., 1997). Barth and Waldner (2002) reported that significantly fewer bulls with body condition scores of 2.0 produced semen categorized as "satisfactory" (minimum sperm motility of 30% and minimum sperm morphology of 70% normal sperm cells) compared to bulls with moderate body condition scores (3.0 to 3.5). Coulter et al. (1997) reported lower sperm motility and a lower proportion of normal sperm in growing bulls fed high energy diets compared to bulls fed moderate energy diets. Coulter and Bailey (1988) suggested that excessive fat deposited in the neck of the scrotum and scrotal tissue may limit adequate heat dissipation resulting in detrimental effects on semen motility and morphology. It is generally observed that a positive genetic and phenotypic association between subcutaneous fat depth and RFI exist, such that low-RFI animals are leaner compared to their high-RFI counterparts (Schenkel et al.. 2004; Nkrumah et al., 2007; Lancaster et al., 2009a,b). Relationships between RFI and fat accretion in beef cattle could also impact semen quality traits.

Growing evidence to suggest that measuring phenotypic RFI of a contemporary group of heifers that includes both pre- and post-pubertal animals will result in later-maturing heifers being ranked as more efficient compared to earlier-maturing heifers, as they have additional energy demands associated with sexual development and activity

(Basarab et al. 2011). It is reasonable to assume that bulls reaching puberty may experience increased energy demands associated with sexual activity and development; however it remains unclear whether or not age of puberty will affect RFI in bulls. Inclusion of RFI as a component of a multi-trait selection program has the potential to improve the profitability of beef production systems with minimal effects on performance traits. However, further research is warranted to further explore associations between RFI in bull fertility traits in growing bulls.

Postweaning and Mature Cow Feed Efficiency

Traditionally, the beef industry has put more selection emphasis on output traits like ADG, in an effort to increase beef productivity outputs. Ratio-based traits that are a measure of feed consumed per unit of weight gain (F:G or feed conversion ratio; FCR) or the inverse (G:F) are genetically associated with growth and mature body size such that selection based on these triats will result in cows with greater mature body size and maintenance energy requirements (Herd and Bishop, 2000; Arthur et al 2001c). Feed is the single largest variable expense associated with the production of beef, and accounts for approximately 65% of total expenses required to maintain a breeding herd (Arthur et al., 2004; Van der Westhuizen et al., 2004). With feed making up such a significant portion of input costs, a reduction in feed intake while maintaining production would have a substantial impact on profitability.

It has been well established that genetic variation in feed efficiency traits (FCR, F:G, RFI) exists in beef cattle, demonstrating that selection for these traits to improve

efficiency of beef production systems is possible (Arthur et al., 2001a,b; Herd et al., 2003). As stated previously, favorable selection for postweaning F:G would lead to larger mature cow size (Herd and Bishop, 2000, Archer et al., 2002). However, larger cows are not necessarily more cost-effective cows, as they will have increased maintenance energy requirements. Jenkins and Ferrell (1994) examined biological efficiency of cows as feed consumed by the cow relative to weaning BW of her calf. The biological efficiency of 9 breed types were evaluated at differing levels of intake. When nutritional conditions were restricted, breed types with a lower genetic potential for growth and lactation had greater pregnancy rates and calf weaning weights compared to when nutritional conditions were less limited (Jenkins and Ferrell, 1994). DiCostanzo et al. (1991) classified Angus cows into three efficiency (efficient, average, and inefficient) phenotypes based on the difference between actual ADG and expected ADG, which was based on BW and intake. Performance and individual intake of cows was measured at maintenance and ad libitum intake levels. When fed at maintenance level, a negative association was found between ADG and metabolizable energy requirement for maintenance (ME_m), such that cows with lower ME_m requirements gained more weight than expected (DiCostanzo et al., 1991). When fed ad libitum, cows in all efficiency categories retained the same amount of energy, but cows categorized as being inefficient consumed more feed than the efficient and average groups. This study indicates that more efficient cows with lower MEm requirements would be more likely to maintain their BW during situations when forage availability is limited.

Residual feed intake is by definition phenotypically independent of the component traits used to calculate expected feed intake, such as BW and ADG. Previous studies have reported that growing calves with low-RFI phenotypes (< 0.5 SD from mean) consumed 15 to 21% less feed compared to high-RFI calves (> 0.5 SD from mean) during postweaning feeding trials with no impact on performance (Lancaster et al., 2009a,b others). Phenotypic and genetic correlations between RFI and growth traits (e.g., ADG, composition of gain) have been extensively reported in growing animals across multiple diets and environments, however, less information is currently available on the relationships between post-weaning RFI and productivity and efficiency of mature females.

Archer et al. (2002) conducted a study conducted to examine the effects of divergent selection for RFI in mature cows. Mature non-pregnant cows previously phenotyped for RFI as growing heifers were tested for feed efficiency after the weaning of their second calf using the same pelleted ration as during post-weaning test. Phenotypic and genetic relationships between post-weaning and mature cow RFI were 0.40 and 0.98, respectively. Moreover, phenotypic and genetic correlations between post-weaning feed intake and feed intake of mature cows was also high (0.51 and 0.94, respectively). Residual feed intake calculated for mature cows remained strongly correlated with intake but independent of ADG and BW. After 1.5 generations of divergent selection for RFI, Arthur et al. (2005) evaluated cow productivity, reproductive performance, and pre-weaning growth of progeny. No differences in BW were found between the RFI selection lines, but the high-RFI cows significantly higher

BF thickness than low-RFI cows at the beginning of the breeding season. In addition, birth BW, pre-weaning daily gain, and weaning BW of calves from cows selected for divergent RFI were found to be similar. Furthermore, Arthur et al. (2005) reported no significant differences between the RFI selection lines in reproductive performance, including pregnancy rate, calving rate, and weaning rate. However, there was a tendency for cows selected from low RFI to calve an average of 5 d later compared to high-RFI selected cows (Arthur et al., 2005). Lawrence et al. (2011) examined the phenotypic variation in RFI in pregnant beef heifers offered a grass silage diet and reported that heifers with high RFI had 17.1% greater intakes compared to low-RFI heifers. Additionally, there were no differences in body condition score, ultrasonic fat depth and calf birth weight between the divergent groups.

Basarab et al. (2007) examined phenotypic relationships between progeny RFI and maternal productivity in 222 yearling calves and their dams across 10 production cycles. Cows that produced progeny with divergent RFI phenotypes had similar pregnancy, calving, and weaning rates, and produced calves with similar birth BW, pre-weaning ADG and weaning BW. In support of results reported by Arthur et al. (2005), Basarab et al. (2007) found that dams that produced low-RFI progeny consumed 11% less feed compared to dams that produced high-RFI progeny. However, in contrast to Arthur et al. (2005), Basarab et al. (2007) reported greater backfat thickness in dams that produced high-RFI progeny. Dams producing low-RFI progeny calved 5 to 6 d later than cows that produced high-RFI progeny, which was in agreement with results reported by Arthur et al. (2005). Basarab et al. (2007) suggested that the difference in calving dates

was likely due to differences in age at first conception between the divergent RFI groups.

Meyer et al. (2008) examined forage intake of grazing Hereford cows during mid- to late-gestation and lactation that were previously phenotyped as having divergent RFI as growing heifers. Using grazing enclosures, and measuring forage disappearance using a rising plate meter, Meyer et al. (2008) found that pregnant cows classified as having low RFI consumed 21% numerically less forage with no change in BW or BCS during the grazing trial compared to their inefficient counterparts. Additionally, low-RFI cows nursing calves had an 11% numerically lower DMI compared to their high-RFI cows, with no impact on BW and BCS (Meyer et al., 2008). The authors cited insufficient numbers of experimental animals and the high SE associated with the methodology used to quantify forage intake in this study as potential limiting factors to the detection of statistically significant differences in intake of grazing forage between cows with divergent phenotypes for RFI.

Archer et al. (2002) and Arthur et al. (2005) concluded that the strong genetic and phenotypic relationships between intake-related traits from postweaning to maturity present the opportunity to select for more feed efficient cows without negatively impacting production or reproductive efficiency. Additionally, Basarab et al. (2007) indicated that dams producing low-RFI progeny consumed less forage compared to dams producing high-RFI progeny. Meyer et al. (2008) and Lawrence et al. (2011) reported that pregnant beef cattle identified as having low RFI consume less forage compared to their inefficient counterparts. These studies indicate that selection of growing heifers

with favorable phenotypes for RFI will result in females that are more efficient at utilizing feed resources. It is important to note that Arthur et al. (2005) and Basarab et al. (2007) observed potential negative association between age at puberty and RFI. Thus, further research to examine associations between RFI and reproductive traits is warranted.

While Arthur et al. (2005) and Basarab et al. (2007) reported a delay in puberty of only 5 to 6 d in low-RFI females, the effect may be amplified if multiple generations of selection were applied. Several studies since have examined the effects of RFI on age at puberty, age at conception, and productivity in heifers (Shaffer et al., 2011; Basarab et al., 2011; Donoghue et al., 2011) Shaffer et al. (2011) reported a negative linear relationship between RFI and age at puberty such that a 1-unit increase in RFI corresponded to a decrease of 7.5 d in age at puberty. A recent study by Basarab et al. (2011) reported that growing heifer calves with divergent RFI reached puberty at the same age and at the same BW. However, when RFI was adjusted for final ultrasound BF and feeding event frequency, low-RFI heifers reached puberty 13 d later and were 14.5 kg heavier than their high-RFI counterparts. Moreover, when heifers were grouped as pre and post-pubertal, the authors reported that the pre-pubertal heifers consumed 4.7% less feed and had 7.5% more desirable FCR ratios compared to post-pubertal heifers, when ADG, BW, and BF was equal. Heifers that reached puberty near the start of within 30-60 d after the start of the RFI feeding test consumed more feed and had longer feeding event durations compared to later maturing heifers. The authors indicated that selection for low RFI heifers from a group of pre- and post-pubertal heifers may result in

later maturing heifers that lack the additional energy demands associated with sexual development and activity being ranked as more efficient, which may negatively impact fertility (Basarab et al., 2011). It is also reasonable to assume that bulls reaching puberty may experience variable energy demands due to sexual activity and development; however, it is still unclear if those demands impact RFI rank. Crowley et al. (2011) also examined genetic relationships between RFI in growing bulls and beef cow performance and found a negative genetic correlation between age at first calving and RFI, suggesting that selection for improved feed efficiency through RFI may delay the onset of puberty. The authors went on to theorize that a delay in the onset of puberty in low-RFI heifers may be due to more energy being partitioned toward growth instead of reproduction during the performance test.

Selecting for cows with lower maintenance energy requirements and improved feed utilization would greatly reduce costs of production; however, the impacts of selection for RFI on economically relevant traits such as reproductive performance and cow productivity over multiple production cycles are still not fully understood.

Determining Voluntary Intake and Digestibility

Specialized feeding systems such as Calan Gate Feeeders™ and the Growsafe System™ have made the direct measurement of individual animal intake in confinement accurate and reliable, with little interference of animal behavior and insuring complete measurement of feed consumed. However, intake of animals on pasture cannot be

directly measured and instead must be estimated. Obtaining a reliable estimate of voluntary herbage intake in the pasture setting has proven a challenge for researchers.

Herbage intake by grazing ruminants has been estimated by measurements taken from the pasture (Walters and Evans 1979) or by measurements taken from the animal (Chacon et al. 1976; Penning and Hooper, 1985; Dove and Mays, 1991). Walters and Evans (1979) used the sward sampling technique, which is based on the differences of available herbage between pre- and post-grazing, over a short period of time to estimate herbage intake of grazing sheep. While the sward method provides adequate measures of intake on a group basis, it fails to provide individual measures of herbage consumption. Chacon et al. (1976) reported that eating behavior estimates of intake (based on number of eating bites and bite size) was comparable to intake directly measured as the difference of herbage offered and herbage refused. One of the simplest methods of determining forage intake of grazing animals is that of weighing the animals before and after grazing, and intake is determined to be the difference between the weights. While Penning and Hooper (1985) found the weighing technique to be highly related with estimates of intake from chromic oxide (which also has errors associated with the method). This method has great potential for error and is arguably not less labor intensive than other methods. The previously discussed methods have limitations on measurements of between-animal variability and are more suitable for measurements of short-term grazing or for behavioral studies (Dove and Mayes, 1991).

More direct and sometimes invasive approaches to measuring feed intake are available in the form of esophageal and ruminal fistulas which assay the herbage actually

consumed by the animal (Van Soest, 1982; Olson, 1991; Luginbuhl et al., 1994). Esophageal cannulations allow for the direct collection of vegetation as the animal grazes and the rumen evacuation technique requires the removal of all rumen contents before the animal begins to graze (Van Soest, 1982). These techniques insure that the forage sampled is representative of what the animal consumes and complete in quantity. It is necessary to recognize that the intrusiveness of these methods may affect the animals and that maintenance of cannulas can be labor-intensive and require personnel with considerable knowledge. Additionally, samples from esophageal or rumen fistulas have been masticated by the animal, resulting in contamination with saliva and also making it more difficult to identify plant species and parts after they have been consumed. Olson (1991) reported elevated levels of nitrogen (N) and acid detergent lignin (ADL) in forage samples collected from esophageal fistula and rumen evacuation techniques, suggesting that the chemical composition of the forage consumed was not the same as the forage sampled (Van Soest, 1982).

When fecal measures of fecal outputs are required the total fecal collections are necessary. This can be accomplished by attaching fecal bags to the animal which is labor intensive and may introduce error by disrupting normal animal grazing behavior (Van Soest 1982; Dove and Mayes, 1991). An alternative method is to estimate fecal output by the dilution of an indigestible fecal marker (e.g. chromic oxide (Cr_2O_3)). Researchers desiring reliable, less invasive and less labor intensive methods to estimate individual-animal intake and digestibility have adopted the use of orally dosed markers and their

subsequent concentration in the feces to provide estimates of herbage intake or digestibility.

Faichney (1975) listed the requirements for an ideal marker to be: 1) inert, with no physiological effects on the animal or microflora 2) unable to be absorbed or metabolized within the gastrointestinal tract 3) physically similar to the material it is to mark 4) unable to be absorbed and 5) have chemical properties to allow precise quantitative measurements. Generally, the markers examined in the literature do not meet all of these requirements. However, by examining the experimental conditions and goals, selecting the proper marker will result in effective measurements (Galyean 1980; Church 1988). The 2 types of markers used in nutritional studies include internal and external markers. Internal markers are indigestible substances that are naturally found within the feed, for example lignin, silica, and acid-insoluble ash. External markers are substances that are added to the diet or administered directly to the animal, for example chromic oxide, rare-earth elements, and even-chained *n*-alkanes.

Indigestible fractions of feedstuff and forages are the source of internal markers that are inexpensive and convenient when measures of digestibility are the goal. Lignin has traditionally been one of the most the extensively used internal markers in nutritional studies; however, studies indicate that difficulties exist in fecal recovery and quantification of lignin (Fahey and Jung 1983). Fahey and Jung (1983) indicated that apparent digestion of lignin did occur in the rumen and modification of lignin may also occur in the lower gut, which results in low fecal recoveries. Additionally, Van Soest (1982) discussed apparent lignin digestibilities of 20-40% often seen in immature

grasses and forages with low lignin content, and attributed the low recoveries to contamination of lignin with non-lignin factors, loss of immature lignin, formation of soluble phenolic matter, heat damaged feed, and inability to recover finely divided lignin in fecal matter. A review of the literature indicates a general agreement that the use of lignin and an internal marker should be limited to situations where fecal recoveries are confirmed to be high (Van Soest, 1982; Fahey and Jung 1983; Cochran and Adams, 1986; Church, 1988; Titgemeyer, 1997).

The uses of silica and acid-insoluble ash (AIA) as internal markers have yielded variable success. Over-recovery of silica in feces is a common occurrence, especially when animals are on pasture. It is not always possible to determine the source of the additional siliceous ash, although it is likely due to contamination from soil and dust (Van Soest 1982). Acid-insoluble ash has been widely used as a marker as there is little diurnal variation in AIA content of the feces and the assay used to determine the concentration in the feces are accurate. The measurement of AIA can suffer from the same issues as that of measuring silica (contamination from non-biogenic sources) as well as the loss of soluble silica (Van Soest, 1982; Van Soest and Robertson, 1985). The commonly used AIA measurement procedure of Van Keulen and Young (1977) can result in an incomplete recovery of silica because of insufficient acid dehydration due to the use of an acid that is too weak (2N HCl) and a time period that is too short (5 min) (Van Soest, 1982; Van Soest and Robertson, 1985; Van Soest et al., 1991). Additionally, precision of AIA as a marker is compromised when the feed or forage contain low levels of AIA, such as grains and alfalfa (Church 1988). The acid-detergent insoluble (ADIA)

ash procedure is simply determined from the inorganic component remaining after conducting an acid-detergent fiber assay (ADF). Van Soest (1982) indicates that the ADIA procedure overcomes the short comings of the AIA procedure by recovering all silica; however, this technique is still subject to contamination from soil silica.

External markers can be used in 2 different ways, administered at a constant level to facilitate estimates of digestibility, fecal output and intake or they can be administered at pulse dose to study passage rates and flow of digesta (Church 1988). Chromic oxide (Cr_2O_3, Cr) traditionally has been the most commonly used external marker, as it does not associate with either the fluid phase or the particulate phase of the digesta and therefore is most suited as a marker of digestibility (Van Soest 1982; Titgemeyer 1997). The most common method of estimating intake based on the use of Cr_2O_3 is to use the chromium to estimate fecal output and in the in vitro digestibility method to measure the digestibility of the diet. Errors in this technique can arise from the application of a single herbage digestibility number to all animals and because method of determining digestibility ignores possible interactions between dietary components (Dove and Mayes 1996; Malossini et al., 1996). The chromium method is criticized as it often produces unrepresentative marker concentrations in the feces due to diurnal variation (Van Soest 1982; Church 1988; Dove and Mayes 1991; Titgemeyer 1997). Sampling feces at various times during the day can help to overcome the issue of diurnal variation. Additionally, minimizing variation arising from the dosing schedule and from temporal sequestration of Cr_2O_3 in the rumen (which results in poor mixing with digesta) can be accomplished by using an intra-rumen controlled-release device (CRD). Use of a CRD

assumes that the marker will be released into the rumen at a constant rate. Adams et al. (1991) found estimates of fecal output using a continuous release marker device containing Cr_2O_3 to be within 1 to 10% of that acquired using a total fecal collection method in grazing beef steers. While the chromium oxide/in vitro method may give adequate estimates of intake, the error arising from the application of a single digestibility coefficient makes this method better suited for predicting intake on a group-basis.

Ytterbium (Yb) is a rare-earth element that has been used to estimate fecal output in sheep and cattle (Coffey et al., 1988; Estell et al., 1990; Hatfield et al., 1990). Estell et al., (1990) reported an average of 9% over estimation in fecal output compared to the total collection method when using a continuous-release bolus placed in the reticulum of steers consuming alfalfa and alfalfa-concentrate diets. Diurnal variation of fecal concentrations of the marker and difficulty in estimating Yb release rates further complicate the use of Yb as a marker. In addition to the consistent reports of overestimates fecal output, calculating intake using Yb encounters the same problems associated with the use of a single digestibility measurement of the feedstuff for all animals.

Both Cr and Yb have been used with variable success as markers to determine fecal output. These assays require methods to overcome the common problems of diurnal variation and dosing multiple times a day. Using these markers to estimate individual animal intake can be confounded by the common practice of applying a single measurement of digestibility (gathered from in vitro or in vivo estimates of digestibility)

of the forage for all animals, which may not apply to the animals being tested. Recently, researchers have investigated a technique to estimate intake, which is independent of separate measures of digestibility. The use of plant wax components, especially *n*-alkanes have demonstrated much promise for estimating intake in grazing ruminants (Malossini et al., 1996; Reeves et al., 1996; Dove et al., 2002)

N-alkanes are long chained hydrocarbons that are a component of the cuticular wax of plants (Van Soest, 1982; Dove and Mays 1991). While alkanes are not the only component of surface waxes they are widespread across plant species and with the development of gas-liquid chromatography they are easily analyzed (Dove and Mayes 1991; 1996). Dove and Mayes (1991) examined the composition of the alkane fraction in a variety of temperate and tropical plant species and found some common characteristics: 1) The length of the main carbon chains detected ranged from 25 to 35; shorter chained alkanes were present in smaller concentrations 2) In all species examined odd-numbered alkanes are present in greater amounts than even-numbered alkanes 3) Alkanes C_{29}, C_{31}, and C_{33} were the dominant alkanes in all species with relative profiles differing across species.

When using n-alkanes to estimate intake, animals are dosed with a synthetic even-numbered alkane (e.g. C_{32}) and consume pasture plants with a certain profile of naturally occurring odd-numbered alkanes. Voluntary herbage intake can then be calculated from the alkane dose, the concentration of alkane in the herbage, and the ratio of the dosed and natural alkanes in the feces (see the following equation):

$$\mathrm{I} = \frac{\mathrm{Fi}}{Fj}\mathrm{Dj}/\left(\mathrm{Hi} - \frac{\mathrm{Fi}}{\mathrm{Fj}}\mathrm{Hj}\right)$$

where I is intake, Hi and Fi are the herbage and fecal concentrations of the odd-chained alkane (naturally occurring) respectively, Hj and Fj are the concentrations of the even-chained (dosed) alkane and Dj is the daily dose of the even-chain alkane.

It is accepted that alkanes do not recover completely and previously reported recovery rates ranged from 0.79 to 1.14 for C_{31}, C_{32} and C_{33} alkanes (Dove and Mayes 1996; Dove et al., 2002; Molina et al., 2004; Ferriera et al., 2007). Generally, in ruminants, the recovery of n-alkanes increases with chain length (Dove and Mayes 1991; Brosh et al., 2003; Ferreira et al., 2007). However, Molina et al. (2004) reported no increase in recovery with greater chain length. Incomplete recoveries of dosed and natural alkanes in the feces indicate that disappearance is occurring in the digestive tract of ruminants. Mayes et al. (1988) reported that the most disappearance of alkanes occurred in the small intestine of sheep, suggesting that the rumen micro flora do not metabolize alkanes. Even though fecal recoveries of naturally occurring and dosed alkanes are incomplete, alkanes of adjacent chain length have similar recoveries, and therefore the use of paired alkanes (e.g. C_{31}:C_{32}) will minimize the effects of incomplete recoveries (Dove and Mayes, 1991; Dove and Mayes, 1996; Dove et al., 2002).

Knowledge of the botanical composition of the diet of animals on pasture is necessary for understanding animal-performance and animal influences on biomass. Knowledge of the amount of forage consumed by cattle on pasture is imperative as forage is the major cost input in most livestock production systems (Herd et al., 2003). As discussed earlier, each plant species has a unique alkane profile, which makes it

possible for the composition of the diet consumed by the animal to be determined by comparing n-alkane concentrations in the forage with those in the species (Mayes et al., 1986; Dove and Mays, 1991, 1996).

Measures of Individual Animal Intake

A number of studies have evaluated the use of n-alkane markers to estimate DM intake and digestibility of grazing cattle (Mann and Stewart 2003; Molina et al., 2004; Premaratne et al., 2005). Mann and Stewart (2003) reported that intake of tropical forage harvested daily and measured using Calan-gate feeders was comparable to herbage intake calculated by paired alkanes (6.28 ± 0.24 vs. 6.21 ± 0.15 kg/d, respectively) in yearling bulls grazing tropical pasture. A study conducted with Angus steers compared n-alkane estimated intake of diets consisting of alfalfa and fescue/alfalfa with actual intakes measured in steers. The authors reported that forage intake estimated from the C_{33}:C_{32} ratio underestimated actual intakes by 4.9 and 0.70% for the alfalfa and fescue/alfalfa diets respectively, although these differences were not significantly different. In agreement with these results, Molina et al. (2004) reported no difference between actual herbage intake of individually fed lactating cows and intake estimated from C_{31}:C_{32} and C_{33}:C_{32} alkanes. Several more studies have found minimal and insignificant discrepancies between known intakes and those using dosed and naturally occurring alkanes (ranging from 0.07 to 0.10 kg/d, Mayes et al., 1986; Dillon and Stakelum 1989; Stakelum and Dillon 1990) all of which suggest that accurate group estimates of herbage intake can be obtained using the paired alkane method. However,

research regarding the use of n-alkanes to determine individual-animal variation in intake has been variable.

Olivan et al. (2007) compared measured intakes of non-lactating non-pregnant mature beef cows consuming alfalfa hay at a low feeding level (1.057 kg DM/100 kg BW per d) and a high feeding level (1.7616 kg DM/100 kg BW per d). The best coefficient of determination ($r^2 = 0.74$) between alkane estimated intake and measured intake values was observed for animals at the low feeding level with the alkane pair C_{25}:C_{24}, where the mean intake was overestimated by 127.9 g/d. Hendrickson et al. (2002) found similar regression parameters for measured and estimated values for voluntary intake of Brahman-cross steers consuming buffel-grass hays using the alkane pairs C_{31}:C_{32} and C_{33}:C_{32} ($r^2 = 0.73$ and 0.72, respectively). In both of the previously discussed studies, the variation between apparent digestibility and subsequent recovery in the feces of n-alkanes was an important limitation of the use of the method to predict individual-animal intakes (Hendrickson et al., 2002; Olivan et al., 2007).

The computation of RFI depends on accurate measurements of DMI and growth of the animal (Koch et al., 1963). The majority of the research on animals with divergent feed efficiencies has been conducted in confinement with prepared feeds where direct measurements of individual animal intake can be collected. Due to the difficulty of estimating intake in grazing animals many results from confinement trials have been assumed to be directly applicable to pasture. Reliable estimates of intake are necessary for the calculation of RFI in grazing cattle and to compare intakes of cattle already identified as having divergent RFI. An Australian study used dosed alkanes contained in

an intraluminal controlled-release device to estimate intake and DM digestibility in 41 lactating cows that had been previously identified as having divergent RFI as growing heifers (Herd et al. 1998). Results from this study found no differences in selectivity of plant component between divergent RFI groups and no differences in forage DMI between high- and low-efficiency cows while grazing. However, they attributed the error to imperfect adjustments for differences in recovery by using previously published recoveries. Another study by Herd et al. (2002) used alkanes to estimate DM digestibility and intake in 53 Angus steers grazing pasture following 1 generation of divergent selection for RFI. No differences were found between DMI, digestibility, or diet selection between the divergent groups, however the low-RFI steers had a more favorable FCR and a greater ADG than steers selected from high-RFI.

The use of alkane marker technology to predict forage intake of specific populations has been effective. However, limited research findings have been conducted to assess the use of alkane marker technology to accurately measure forage intake of individual animals for the purpose of genetic improvement in feed efficiency (Arthur et al., 2004). The challenge still remains to refine and develop the use of alkanes to accurately provide assessments of voluntary forage intake to identify animals that are divergent in ability to efficiently utilize grazed forages.

Associations of Residual Feed Intake and Digestibility

Factors that influence digestibility include but are not limited to level of intake, passage rate, environmental conditions, breed difference, and dietary characteristics

(Church, 1988). In ruminants, it is generally accepted that as level of intake increases digestibility decreases, therefore high-RFI cattle that have greater intakes may have lower apparent dry matter digestibility (DMD) due to level of intake. Various methods have been used to measure digestibility in beef cattle (Nkrumah et al; 2006; Cruz et al., 2010; McDonald et al., 2010) and sheep (Redden et al., 2010) with divergent feed efficiency, with variable results.

Richardson et al. (1996) reported that low-RFI steers had 1% greater DM digestibility compared to high-RFI steers, and those small differences in digestibility may contribute to differences in between-animal variation in RFI. Nkrumah et al. (2006) measured apparent digestibility of DM, CP, ADF and NDF in 27 steers fed at 2.5 times estimated maintenance requirements using the total fecal collection method. No significant differences were found between steers identified as having low, medium or high-RFI. However, a tendency for a negative association between RFI and digestibility of dietary CP (-0.34) and DM (-0.33) was reported, such that greater DM and nutrient digestibility was associated with more efficient animals. Steers with low RFI were observed to have numerically greater DM digestibility (4.5 percentage units), compared to steers with high RFI. In agreement, Kruger et al. (2009) found negative associations of RFI with DM, NDF, ADF and CP and mineral (P, Ca, Zn, and Cu) digestibility in Brangus heifers, with low-RFI heifers had 3.7% greater DM digestibility compared to high-RFI heifers. McDonald et al. (2010) reported a high negative correlation (-0.51) between RFI and diet DM digestibility, such that low-RFI cows had greater a greater DM digestibility compared to high-RFI cows (74 vs 63%, respectively). McDonald et al.

(2010) used indigestible ADF to estimate DM digestibility of mature mid-gestation cows fed a diet of 74% grass hay and 26% grain-based supplement. The cows were previously identified as having divergent phenotypes for RFI as growing heifers. McDonald et al. (2010) reported a strong negative correlation (-0.51) between RFI and diet DM digestibility, such that low-RFI cows had greater DM digestibility compared to high-RFI cows (74 vs 63%, respectively).

Other studies have reported no differences in digestibilities in beef cattle and ewes with divergent RFI. Richardson et al. (2004) used total fecal collections to determine DM digestibility in 16 steers with divergent RFI, but reported no differences between efficient and inefficient animals. Cruz et al. (2010) used lignin as an internal marker to calculate DM digestibility in 30 Angus x Hereford crossbred steers fed a corn based finishing ration and found no differences in DM digestibility between divergent RFI groups. However, it is important to note that a period of 60-d was used to measure RFI, which is less than the recommended 70 d (Archer et al., 1997), which may have reduced accuracy for predicting individual intake and growth. Additionally, the use of lignin as a marker to measure digestibility was likely not appropriate for the corn-based diet, due to the incomplete fecal lignin recovery often seen in high concentrate diets (Van Soest 1982). Despite the lack of significance, digestibility of low-RFI steers were numerically greater by 1 and 4 % units compared to high-RFI steers (Cruz et al., 2010). Finally, Redden et al. (2010) reported no difference in digestibility among divergent RFI groups of yearling ewes previously phenotyped for RFI as growing lambs.

Due to the conflicting reports regarding differences in digestibility in beef cattle with divergent RFI, more research is needed to determine the amount of variation in feed efficiency that can be accounted for by digestion of nutrients. It is important that research select methods (markers) for measuring digestibility carefully, to insure they are appropriate for the diet type and conditions of the research.

Conclusions and Objectives

Constantly increasing input costs coupled with social pressures for improved sustainability leave researchers and producers with the challenge of increasing efficiency of production without impacting the quality or quantity of product. Residual feed intake is a feed efficiency trait that has the potential for selection of beef cattle with improved utilization of feed with no impact on growth and BW. However the genetic, physiological, and biological mechanisms that contribute to variations in RFI in cattle have yet to be fully understood. Additionally, the impacts of selection for RFI on other economically important traits such as female productivity and male fertility have yet to be thoroughly investigated. Finally, improvement and expansion on methods of measuring feed intake are imperative to furthering the understanding of RFI throughout the production cycle. Therefore the objectives of this study were threefold: 1) To characterize feed efficiency traits and examine phenotypic correlations with performance, scrotal circumference and semen-quality traits in growing bulls 2) To characterize residual feed intake in developing beef heifers and examine relationships with growth, carcass composition, energy metabolism and the subsequent intake and

efficiency of forage utilization of mid-gestation females 3) To examine the relationships between residual feed intake and apparent diet digestibility in growing heifers and mid-gestation cows and 4) To evaluate the use of n-Alkanes as a method to accurately predict individual-animal intake and digestibility in mid-gestation cows selected for divergent feed efficiency.

CHAPTER II

RELATIONSHIPS BETWEEN FEED EFFICIENCY, SCROTAL CIRCUMFERENCE AND SEMEN-QUALITY TRAITS IN GROWING BULLS*

Introduction

Feed cost is the single largest variable expense associated with the production of beef, and accounts for approximately 65% of the expense required to maintain a breeding herd (Arthur et al., 2004; Van der Westhuizen et al., 2004). Ratio-based traits like G:F have been used to measure feed efficiency, but favorable selection will result in increased growth and mature cow size. Residual feed intake (RFI) is a measure of feed efficiency that is independent of growth traits (Herd and Arthur, 2009) and moderately heritable (Herd et al., 2003). Progressive seedstock producers are adopting technology to measure daily intake to assess feed efficiency of growing bulls and heifers. Inclusion of RFI in selection indexes will enable selection for feed efficiency with minimal effects on growth and other performance traits.

Studies have indicated that heifers with low-RFI phenotypes may have delayed onset of puberty (Arthur et al., 2005; Basarab et al., 2007; Shaffer et al., 2011; Basarab

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et al., 2011). Basarab et al. (2011) suggested that measuring phenotypic RFI in postweaning heifers will favor later-maturing heifers as they have less additional energy demands associated with sexual development and activity. While the mechanisms by which RFI influences age of puberty in females is still unclear, it is important to examine what impact this selection may have on male fertility.

Scrotal circumference (SC) is correlated with sperm production and is an important when evaluating breeding soundness of young bulls (Hahn et al., 1969; Lunstra and Echternkamp, 1982; Gipson et al., 1985). Previous studies have reported that SC is not associated with RFI in growing bulls (Schenkel et al., 2004; Arthur et al., 2001a), however few studies have examined the association of semen-quality traits and RFI in cattle. This study was conducted to characterize feed efficiency traits and examine phenotypic correlations with performance, scrotal circumference and semen-quality traits in growing bulls.

Materials and Methods

Experimental Animals and Design

All procedures were approved by the Institutional Animal Care and Use Committee of Texas A&M University, prior to the initiation of each trial. Five postweaning trials utilizing Angus (n = 92), Bonsmara (n = 62), and Santa Gertrudis (n = 50) bulls were conducted at the Beef Development Center (Millican, TX), McGregor Research Center (McGregor, TX), O.D. Butler Jr. Animal Science Complex (Texas A&M University College Station, TX), and the Beef Systems Research Center (Texas

A&M University College Station, TX) to measure performance, feed efficiency, and breeding soundness traits in growing bulls. Bonsmara is a subtropically adapted Bos Taurus composite composed of approximately 60% Africaner, and 20% each of Hereford and Shorthorn breeds (Corbet et al., 2006).

The Bonsmara bulls located at the McGregor Research Center (Trial 1), and Angus bulls at the O. D. Butler Jr. Animal Science Complex (Trials 3 and 4) were stratified by BW and randomly assigned to pens each equipped with 4 or 6 Calan-gate feeders (American Calan, Northwood, NH), whereas, the Angus bulls at the Beef Development Center (Trial 2) and Santa Gertrudis bulls at the Beef Research Unit (Trial 5) were randomly assigned to pens equipped with 9 or 4 GrowSafe feed bunk units (GrowSafe Systems Ltd., Airdrie Alberta, Canada). For all trials, bulls were allowed a minimum of 24 d to adapt to experimental diets, which ranged from 1.70 to 2.85 Mcal ME/kg and 12.4 to 13.5% CP (DM basis; Table 2.1). Bulls in Trials 2, 3, 4 and 5 were fed ad libitum twice daily, whereas, bulls in Trial 1 were fed ad libitum once daily.

Individual intakes were measured using the Calan gate system for 70 or 77 d during Trials 1, 3 and 4. During Trials 2 and 5, individual intakes were recorded for 70 and 77 d, respectively, using the GrowSafe™ Data system (DAQ 4000E). Procedures for filtering feed intake data collected from the GrowSafe feeding system (e.g., equipment malfunction or assigned feed disappearance) for Trials 2 and 5 were previously reported (Lancaster et al., 2009). Bulls were weighed at 14-d intervals, and hip height (HH), scrotal circumference (SC), and real-time ultrasound measurements of 12^{th} rib fat thickness (BF) and longissimus muscle area (LMA) obtained at the start and end of each

Table 2.1. Composition and analyzed nutrient content of the diets fed to growing bulls

Item	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5
Dietary composition, % (as-fed basis)					
Chopped alfalfa hay	-	-	35.0	12.8	35.0
Pelleted alfalfa hay	-	-	15.0	3.2	15.0
Dry rolled corn	13.5	-	-	-	19.5
Corn silage	-	30.0	-	-	-
Cracked corn	-	49.0	19.5	74.8	-
Cotton seed hulls	50.0	7.0	21.5	2.1	21.5
Cotton seed meal	14.5	5.0	-	-	-
Ground milo	13.5	-	-	-	-
Molasses	6.0	4.5	7.0	4.3	7.0
Supplement[1]	2.5	4.5	2.0	2.8	2.0
Chemical composition (DM basis)[2]					
DM, %	91.6	68.6	88.3	88.9	88.0
ME, Mcal/kg of DM[1]	1.70	2.73	1.95	2.85	2.07
CP, % of DM	12.4	13.5	13.4	13.1	13.1
NDF, % of DM	52.2	26.3	47.3	17.5	32.0

[1]Supplement contained salt, urea (only in trial 4, 1.17% dietary composition, as-fed), vitamin E (44,000 IU/kg product), vitamin A (2,200,000 IU vitamin A/kg) vitamin D (440,000 IU vitamin D/kg product), vitamin E (8,800 IU vitamin E/kg product, and a trace mineral containing a minimum of 19.0% Zn, 7.0% Mn, 4.5% Cu, 4,000 mg/kg Fe, 2,300 mg/kg I, 1,000 mg/kg Se, and 500 mg/kg Co

[2]Chemical analysis was conducted by an independent laboratory (Cumberland Valley Analytical Services Inc., Hagerstown, MD). ME concentrations were computed using the Cornell Net Carbohydrate and Protein System (version 5.0, Cornell University, Ithaca, NY)

trial by an Ultrasound Guidelines Council field-certified technician using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer (Corometrics Medical Systems Inc., Wallingford, CT). Ultrasound images were sent to the National Centralized Ultrasound Processing laboratory (Ames, IA) for analysis.

Breeding soundness examinations (BSE) were conducted 5, 34, 2, 51, and 25 d following the conclusion of Trials 1, 2, 3, 4, and 5, respectively, when bulls ranged from 365 to 444 d of age. Semen was collected using a programmable electroejaculator, and semen samples visually assessed to determine sperm motility. Semen samples were retained for later evaluation of semen morphology. Bulls were given a BSE score as satisfactory or unsatisfactory for breeding based on minimum criterion for SC, sperm motility, and sperm morphology as recommended by the Society of Theriogenology (Chenoweth et al., 1992).

Diet ingredient samples were collected weekly throughout the study and composited by weight for chemical analysis. Moisture analysis was conducted by drying in a forced-air oven for 48 h at 105 C (AOAC, 1995), and chemical analysis conducted by an independent laboratory (Cumberland Valley Analytical Services Inc., Hagerstown, MD). Ingredient and chemical composition of the experimental diets are presented in Table 2.1.

Computations and Statistical Analysis

Growth rates of individual bulls were modeled by linear regression of 14-d BW against day of the trial using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC) and regression coefficients used to compute ADG, initial and final BW, and metabolic BW

(MBW; mid-test $BW^{0.75}$). Moisture analysis was used to calculate average daily DMI from feed intake data. Three feed efficiency traits were calculated for each animal including G:F (ADG divided by DMI), RFI unadjusted (RFIp) and RFI adjusted for inter-animal variation in carcass composition as measured by ultrasound (RFIc). Unadjusted RFI was calculated as actual DMI minus DMI expected to meet growth and maintenance energy requirements (Koch et al., 1963). Expected DMI was calculated by linear regression of DMI on MBW and ADG, using a mixed model (SAS Inst. Inc.), with trial and trial by independent variable interactions included as random effects and the variance component option used for the variance-(co)variance matrix structure:

$$Y_{ij} = \beta_0 + \beta_1 MBW_{ij} + \beta_2 ADG_{ij} + \beta_3 \tau_i + (\beta_4 MBW_j \times \tau_i) + (\beta_5 ADG_j \times \tau_i) + \beta_{x1} X_{ijk} + (\beta_{x2} X_{jk} \times \tau_i) + e_{ij},$$

where Y_{ij} is the standardized DMI of the jth bull in the ith trial, τi is the random effect of the ith trial, X_{ijk} is the kth ultrasound composition trait for the jth bull in the ith trial, β_0 is the regression intercept, β_1 is the regression coefficient on MBW, β_2 is the regression coefficient on ADG, β_3 is the regression coefficient on random trial, β_4 is the regression coefficient on the random interaction of MBW and trial, β_5 is the regression coefficient on the random interaction of ADG and trial, β_{x1} is the regression coefficient on the kth ultrasound composition trait, β_{x2} is the regression coefficient on the random interaction of the kth ultrasound composition trait and ith trial, and e_{ij} is the uncontrolled error for the jth bull in the ith trial.

Stepwise regression analysis (PROC REG of SAS) was performed to determine the order of inclusion of ultrasound-carcass traits in the base model to compute carcass-adjusted RFI (RFIc). Ultrasound-carcass traits were sequentially added to the base model in the order determined by the stepwise regression analysis, and the change in the resulting coefficient of determination used to establish their relative importance to account for additional variation in DMI. Results from these analyses were used to determine the inclusion of ultrasound measurements of carcass composition to calculate expected DMI. An additional RFI trait (RFIc) was computed from expected DMI adjusted for carcass composition as well as for MBW and ADG.

The MIXED procedure of SAS was used to adjust age, performance and feed efficiency (excluding RFIp and RFIc) traits, ultrasound measures of carcass composition, and scrotal circumference for the random effect of trial. Dependent variables were analyzed using a one-way random effect treatment structure with trial as a random effect (Littell et al., 2006) and an adjusted variable calculated as the overall mean plus the residual. Phenotypic correlation coefficients (CORR procedure of SAS) were generated among adjusted variables and breeding soundness examination parameters. Bulls were classified into low, medium, and high-RFI phenotype groups that were < 0.5, ± 0.5 and > 0.5 SD, respectively, from the mean RFIp of 0.00 ± 0.90 kg/d. A general linear model (MIXED procedure of SAS) was used to examine the fixed effect of RFIp group on performance, feed efficiency and ultrasound carcass composition traits, and scrotal circumference. Comparisons of least square means between RFIp groups were performed using Tukey's post hoc test. A generalized linear mixed model

(GLIMMIX procedure of SAS) was used to examine the effect of RFIp group on percent normal sperm and percent motile sperm with a Poisson distribution and the default log option used for the link function. Breeding soundness exam score was analyzed using Chi-square (FREQ procedure of SAS) analysis.

Results and Discussion

The initial age of the bulls averaged, 321 d across the 5 trials and ranged from 291 d in Trial 1 to 353 d in Trial 3 (Table 2.2). Initial BW averaged 309 kg and ranged from 265.7 in Trial 5 to 352.8 kg in Trial 3. Bulls in Trial 2 had the least ADG (0.95 kg/d) and DMI (8.52 kg/d) compared to bulls during the other 4 trials. The lower performance of these bulls likely reflects the fact that this trial was conducted in the summer (June to July), whereas, the other trials were conducted from January to March when environmental conditions were more favorable. Gain to feed ratio ranged from 0.11 for Trials 2 and 3 to 0.17 for Trial 4. The SD for RFI were 1.09, 0.71, 0.91, 0.77, and 1.06 kg/d for Trials 1 through 5, respectively, which are within the range of SD for RFI previously reported for growing cattle fed high-roughage diets (0.74 to 1.47 kg/d; Arthur et al., 2001b,c; Schenkel et al., 2004), and high-concentrate diets (0.66 to 0.83 kg/d; Basarab et al., 2003; Nkrumah et al., 2004).

Previous studies (Herd and Bishop, 2000; Arthur et al., 2003; Basarab et al., 2003; Schenkel et al., 2004; Nkrumah et al., 2007) have included trial as a fixed effect in models to compute RFI in order to adjust for intercept differences due to trial, but did not consider trial×independent variable (ADG, MBW) interactions to adjust for potential

Table 2.2. Summary statistics of performance, feed efficiency, ultrasound composition, scrotal circumference, and semen-quality traits of growing bulls

Trait[1]	Trial 1		Trial 2		Trial 3		Trial 4		Trial 5	
No. bulls	62		48		17		27		50	
Breed	Bonsmara		Angus		Angus		Angus		Santa Gertrudis	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Initial age, d	291	10.7	309	47.3	353	10.3	324	10.6	333	21.6
Age at BSE, d	3652	10.7	412	47.3	432	10.3	444	10.6	417	21.6
Initial BW, kg	258	30.4	361	55.5	367	22.9	298	34.4	266	34.9
Final BW, kg	382	37.2	427	63.0	469	22.8	385	39.6	357	36.9
ADG, kg/d	1.77	0.20	0.95	0.28	1.32	0.20	1.78	0.26	1.30	0.21
DMI, kg/d	11.1	1.67	8.5	1.27	11.9	1.15	10.2	1.25	10.1	1.11
G:F, kg/kg	0.16	0.02	0.11	0.02	0.11	0.01	0.17	0.02	0.13	0.02
RFIp, kg/d	0.00	1.09	0.00	0.71	0.00	0.91	0.00	0.77	0.00	1.06
Final BF, cm	0.56	0.68	0.57	0.18	0.76	0.18	0.58	0.16	0.27	0.02
Final LMA, cm^2	61.6	8.0	70.6	10.2	75.2	6.8	72.9	7.1	60.9	6.02
Final HH, cm	124	3.4	125	3.9	123	3.2	122	4.0	123	4.3
Initial SC[2], cm	24.5	2.5	28.7	3.1	34.6	2.3	32.0	3.01	--	--
Final SC, cm	31.0	2.3	32.8	2.7	36.9	1.8	36.8	3.3	34.0	3.2
Normal sperm, %	64.2	17.9	72.8	20.4	70.7	22.2	90.8	20.0	87.4	5.8
Sperm motility, %	23.7	18.0	48.2	27.1	40.8	14.2	43.3	18.1	30.4	22.4

[1]Initial age = age at start of trials; Age at BSE = age at time breeding soundness examination conducted; RFIp = residual feed intake, BF = 12th-rib backfat thickness; LMA = longissimus muscle area; HH = hip height; SC = scrotal circumference

[2]Data not available for initial scrotal circumference for trial 5

slope differences in DMI among trials. Trial is fundamentally a random variable given that inference is to be made about future trials. Thus, the variation attributable to trial×independent variable interactions should be considered when computing RFI across multiple trials. St-Pierre (2001) indicated that including the effect of trial and trial×independent variable interactions is important to avoid bias of the residual, when performing regression across multiple trials. In the current study, multiple breeds were examined across trials using 2 types of intake-measurement systems (GrowSafe system vs Calan gate) with the trials conducted at multiple sites and mo of the year. Despite these differences between trials, the inclusion of trial and trial×independent variable (MBW and ADG) interactions as random effects (Random-effects model) in the model to compute RFIp only slightly improved the R^2 compared to the trial fixed-effect model (trial only; R^2= 0.672 vs. 0.662, respectively). Lancaster et al. (2009a) and Lancaster et al. (2009b) also compared a random-effects model (trial×independent variable interactions) with a trial fixed-effect model to determine RFIp in growing heifers and bulls. In both studies, the random-effects model accounted for little additional variation in DMI (R^2 = 0.555 vs. 0.546 for heifers; 0.803 vs. 0.802 for bulls, respectively) compared to with the trial fixed-effect model.

Stepwise regression analysis using the trial fixed-effect model revealed that final BF accounted for additional variation in DMI (R^2 = 0.676 vs 0.662), although the other ultrasound carcass composition traits (initial BF and LM area, gain in BF and LM area and final LM area) were not significant ($P > 0.11$). The increase in variation in DMI attributed to final BF in this study was slightly less than in previous studies (Arthur et al.

2003; Basarab et al. 2003; Lancaster et al 2009b; Kelley et al. 2010), which reported that carcass-fat traits accounted for 2 to 4% of additional variation in DMI not explained by MBW and ADG. Furthermore, the inclusion of final BF in the random-effects model accounted for more variation in DMI compared to when final BF was added to the trial fixed-effect model (R^2 = 0.703 vs. 0.676). Lancaster et al. (2009a) also found that the additional variation in DMI attributed to carcass fat beyond that explained by MBW and ADG was larger when the model included trail and trial x independent variables as random effects compared to when trial was included as a fixed effect. These results suggest that the inclusion of trial and trial × independent variable interactions as random effects may be more appropriate when additional variables beyond MBW and ADG are being considered in models to calculate RFI.

Means of final scrotal circumference ranged from 31.0 to 36.9 cm across the 5 trials. Initial and final SC were the lowest (24.5 and 31.0 cm, respectively) for Bonsmara bulls (Trial 1) that were also younger and lighter compared to the bulls in the other 4 trials. The Angus bulls in Trial 3 had the largest initial SC (34.6 cm) and were the oldest and had the heaviest initial BW at the start of the trial. Numerous studies have reported that BW and ADG are favorably correlated with SC in growing bulls (Barber and Almquist 1975; Bourdon and Brinks 1986). The proportion of sperm with normal morphology ranged from 64.2% in Bonsmara bulls to 90.8% for Angus bulls in Trial 4 (Table 3.2), and reflects possible differences in breed as well as age. Fields et al. (1982) reported that the proportion of morphologically normal sperm increases with bull age. Bonsmara bulls were 12 mo of age while the Angus and Santa Gertrudis bulls were

between 14 and 15 mo of age when BSE examinations were conducted. Normal sperm percentages measured in this study were within the range of 44 to 90% reported by Fields et al. (1982) and Tatman et al. (2004) for bulls of similar age. Progressive sperm motility ranged from 23.7% for Bonsmara bulls in Trial 1 to 48.2% for Angus bulls in Trial 2, which were within the range of 8 to 60% reported in previous studies (Fields et al., 1982; Tatman et al. 2004).

Phenotypic correlations among trial-adjusted growth and feed efficiency traits are presented in Table 2.3. Dry matter intake was positively correlated with initial BW (0.40) and ADG (0.60), and both RFI traits (0.71 and 0.69 for RFIp and RFIc, respectively), which are consistent with results from previous studies (Herd and Bishop, 2000; Hoque et al., 2005; Nkrumah et al., 2007; Lancaster et al., 2009b). Both RFIp and RFIc were negatively correlated with G:F (-0.70 and -0.68, respectively), indicating that selection for RFI would also result in more desirable G:F (Lancaster et al., 2009b; Kelley et al., 2010). As expected, RFIp was independent of initial BW and ADG, such that bulls with low RFIp (< 0.50 SD from mean RFIp) phenotypes consumed 20% less DMI than bulls with high RFIp while ADG, HH, and final BW were similar (Table 3.5). Numerous studies have found RFIp to be genetically independent of growth and BW in beef cattle (Archer et al. 1997; Arthur et al. 2001b,c; Basarab et al. 2003; Nkrumah et al. 2004; Nkrumah et al. 2007; Crowley et al., 2011), although weak genetic correlations have been reported in several studies (Herd and Bishop, 2000); Schenkel., 2004). Bulls with low RFIp had 10% less final BF, but similar LM area compared to high-RFIp bulls,

which is in agreement with previous studies in growing beef cattle (Arthur et al., 2003; Basarab et al., 2003; Nkrumah et al., 2007; Kelly et al., 2010a).

Phenotypic correlations among feed efficiency and fertility traits are presented in Table 2.4. Gain in SC was positively correlated with ADG (0.28), and initial and final SC were positively correlated with DMI (0.27 and 0.22) and final BF (0.22 and 0.20, respectively). Bourdon and Brinks (1986) also reported a phenotypic correlation of 0.25 between SC and postweaning ADG in Hereford bulls. In a study with growing bulls involving multiple breeds, Schenkel et al. (2004) found that SC was genetically correlated in a positive manner with DMI (0.33), ADG (0.24) and final BF (0.19).

Although gain in SC was negatively correlated phenotypically with G:F (-0.28), final SC was not correlated with G:F or either of the RFI traits. In fact, bulls with divergent RFIp phenotypes had similar initial and final SC and gain in SC (Table 2.5). In agreement with this study, Arthur et al. (2001a) and Schenkel et al. (2004) found that final SC was phenotypically and genetically independent of RFI in growing bulls. Crews et al. (2006) derived a 3-trait selection index for growing bulls based on RFI, ADG and 365-d yearling BW to predict genetic merit for net revenue of feedlot progeny. The index value was favorably correlated with RFI, DMI and ADG (0.74, -0.22 and 0.53, respectively), but was not correlated with yearling BW, such that high index bulls consumed less DMI, gained faster and had similar yearling BW compared to bulls with low index values. The selection index tended to be positively correlated with SC (0.16), which likely reflects the positive association between SC and ADG. These results

Table 2.3. Phenotypic correlations among trial-adjusted growth, feed intake, and feed efficiency traits in growing bulls

Trait[1]	Initial BW	ADG	DMI	G:F	Final BF	RFIp	RFIc
Initial age	0.32*	-0.04	0.04	-0.11	0.17*	-0.06	-0.07
Initial BW		0.16*	0.40*	-0.17*	0.12†	-0.01	-0.01
ADG			0.60*	0.60*	0.36*	0.01	0.01
DMI				-0.26*	0.43*	0.71*	0.69*
G:F					-0.03	-0.70*	-0.68*
Final BF						0.20*	0.01
RFIp							0.98*

[1]Initial age = age at start of trials; BF = 12th-rib backfat thickness; RFIp = residual feed intake; RFIc = carcass-fat adjusted RFI

*Correlation coefficient is different from zero at $P < 0.05$

†Correlation coefficient is different from zero at $P < 0.10$

Table 2.4. Phenotypic correlations between trial-adjusted feed efficiency and ultrasound, scrotal circumference, and semen quality traits in growing bulls (n = 154 for initial SC and n = 204 for all other traits)

Trait[1]	ADG	DMI	G:F	Final BF	RFIp	RFIc
Initial SC	0.03	0.27*	-0.20*	0.22*	0.08	0.05
Final SC	0.12†	0.22*	-0.01	0.20*	-0.01	-0.04
Gain SC	0.28*	0.05	-0.28*	0.06	-0.07	-0.07
Normal Sperm	0.01	0.17*	-0.17*	0.16*	0.13†	0.11
Sperm motility	-0.07	0.02	-0.09	0.09	0.01	0.01

[1]BF = 12th-rib backfat thickness; RFIp = residual feed intake; RFIc = carcass-fat adjusted RFI; SC = scrotal circumference.

*Correlation coefficient is different from zero at $P < 0.05$.

†Correlation coefficient is different from zero at $P < 0.10$.

Table 2.5. Effects of residual feed intake (RFIp) classification on performance, feed efficiency, scrotal circumference and semen quality traits of growing bulls

Item[1]	Low RFIp	Medium RFIp	High RFIp	SEM	*P*-value
No. of bulls	50	92	62	--	--
Performance and growth traits:					
Initial BW, kg	301[a]	318[b]	303[a]	5.3	0.01
Final BW, kg	395[a]	414[b]	396[a]	8.1	0.01
ADG, kg/d	1.42	1.44	1.41	0.03	0.66
DMI, kg/d	9.0[a]	10.5[b]	11.2[c]	0.14	0.01
Final hip height, cm	123	124	123	0.54	0.14
Feed efficiency traits:					
G:F, kg/kg	0.16[a]	0.14[b]	0.12[c]	0.01	0.01
RFIp, kg/d	-1.17[a]	-0.01[b]	0.97[c]	0.06	0.01
RFIc, kg/d	-1.11[a]	-0.01[b]	0.91[c]	0.06	0.01
Final ultrasound traits:					
BF, cm	0.57[a]	0.62[b]	0.63[c]	0.02	0.03
LMA, cm^2	67.6	68.7	67.7	1.08	0.67
Scrotal circumference:					
Initial SC, cm	29.5	30.1	30.0	0.45	0.54
Final SC, cm	34.0	34.7	33.9	0.38	0.14
Gain in SC, cm	4.4	4.2	4.3	0.27	0.85
Semen quality traits:					
Normal sperm, %	74.0	77.7	77.2	5.27	0.09
Sperm motility, %	34.9	36.5	36.4	3.59	0.34

[1]RFIp = residual feed intake; RFIc = carcass-fat adjusted RFI; BF = 12^{th}-rib backfat thickness; LMA = longissimus muscle area; SC = scrotal circumference

[abc]Means within row with unlike superscripts differ at $P < 0.05$

suggest that multiple-trait indexes that incorporate RFI would not be expected to result in unfavorable selection for low SC.

Sperm morphology was not related to ADG, but was weakly correlated with DMI (0.17) and G:F (-0.17), and final BF (0.16). Moreover, sperm morphology tended to be weakly correlated to RFIp (0.13). This association between sperm morphology and RFIp resulted in low-RFIp bulls tending to have a lower percentage of normal sperm compared to bulls with medium and high RFIp (77.2, 77.7 and 74.0%, respectively). However, when RFI was adjusted for final BF, the magnitude of the association with sperm morphology was reduced. Progressive motility of sperm was not significantly correlated with ADG, DMI, G:F or either of the RFI traits. While this study found no association of sperm morphology with ADG, Siegel et al. (1963) and Marini and Goodman (1969) found that selection for rapid growth was associated with lower percent of normal sperm and lower motility in broilers and bulls. Inadequate body fat has been reported to negatively impact SC, sperm motility and sperm morphology in bulls (Barth and Waldner, 2002), however excess fat has also been associated with decreased sperm production and seminal quality (Mwansa and Makarechian, 1991; Coulter et al., 1997). Barth and Waldner (2002) reported that significantly fewer bulls with body condition scores of 2.0 produced semen categorized as "satisfactory" (minimum sperm motility of 30% and minimum sperm morphology of 70% normal sperm cells) compared to bulls with moderate body condition scores (3.0 - 3.5). Coulter et al. (1997) reported lower sperm motility and a lower proportion of normal sperm in growing bulls fed high energy diets compared to bulls fed moderate energy diets. Coulter and Baiey (1988)

suggested that excessive fat deposited in the neck of the scrotum and scrotal tissue may limit adequate heat dissipation resulting in detrimental effects on semen motility and morphology. In this study, low-RFI bulls were leaner compared to high-RFI bulls (0.57 vs 0.63 cm), which may have contributed to the tendency for low-RFI bulls to have lower percentages of normal sperm.

Morrison et al. (1997) found that multiple generations of divergent selection for RFI in Rhode Island Red chickens did not affect the proportion of normal sperm in cockerels. However, sperm from low-RFI cockerels had greater motility compared to sperm from high-RFI cockerels. Cockerels selected for high RFI had lower mitochondrial content in the sperm cells. Since ATP generate by mitochondria is essential for sperm motility, Morrison et al. (1997) suggested that differences in mitochondrial function may have contributed to the inferior sperm motility in the high-RFI line cockerels.

Breeding soundness scores of bulls with divergent RFIp are presented in Table 2.6. The proportion of bulls that had satisfactory or unsatisfactory BSE scores was not affected by RFI phenotype group. Breeding soundness evaluations were based on minimal requirements for SC at a given age, minimum sperm motility (30% motile sperm), and minimum sperm morphology (70% normal sperm cells; Chenoweth et al., 1992). All three aforementioned measurements were required to assign a breeding soundness score; therefore bulls missing one or more measurements were not assigned a breeding soundness score. Consequently 52 of the 204 bulls evaluated for this study were not assigned a breeding soundness score.

Table 2.6. Chi-Square analysis of breeding soundness exam (BSE) scores of growing bulls with divergent RFIp

Item[1]	Low RFIp	Medium RFIp	High RFIp	*P*-value
Breeding soundness exam score:				
No. bulls receiving BSE score	39	62	51	
No. bulls scored satisfactory (%)	32 (82)	46 (74)	39 (76)	0.35
No. bulls scored unsatisfactory	7 (18)	16 (26)	12 (24)	0.45

[1]RFIp = residual feed intake

Several studies have reported associations between RFI and age of puberty of growing females (Arthur et al., 2005; Basarab et al., 2007; Shaffer et al., 2011; Basarab et al., 2011). Arthur et al. 2005 reported that Angus cows selected for low RFI after 1.5 generations had a tendency to calve 5 d later their high-RFI counterparts. In agreement with this study, Basarab et al. (2007) found that dams of progeny with low RFI calved on average 5 to 6 d later than dams of progeny with high RFI. Furthermore, Shaffer et al. (2011) reported a negative linear relationship between RFI and age at puberty such that a 1-unit increase in RFI corresponded to a decrease of 7.5 d in age at puberty. A recent study by Basarab et al. (2011) found that heifers with low RFI had lower subsequent pregnancy rates compared with heifers with high RFI. However, when RFI was adjusted for ultrasound BF thickness and feeding event frequency, heifers with low RFI had similar pregnancy rates. Growing evidence to suggest that measuring phenotypic RFI of a contemporary group of heifers that includes both pre- and post-pubertal animals will result in later-maturing heifers being ranked as more efficient compared to earlier-maturing heifers, as they have additional energy demands associated with sexual development and activity (Basarab et al. 2011). It is reasonable to assume that bulls reaching puberty may experience increased energy demands associated with sexual activity and development; however it remains unclear whether or not age of puberty will affect RFI in bulls.

Conclusions

Results from this study suggest that RFI is not phenotypically associated with SC or sperm motility, but was weakly associated in an unfavorable manner with sperm morphology in growing bulls. Inclusion of RFI as a component of a multi-trait selection program has the potential to improve the profitability of beef production systems with minimal effects on performance traits. Further research is warranted to further explore associations between RFI in bull fertility traits in growing bulls.

CHAPTER III

RELATIONSHIPS BETWEEN POSTWEANING RESIDUAL FEED INTAKE IN HEIFERS AND FORAGE INTAKE OF MATURE MID-GESTATION FEMALES

Introduction

Traditionally, the beef industry has put more emphasis on output traits like weaning BW and post-weaning ADG in selection programs to improve beef productivity and profitability. The advances made to increase production efficiency in the beef cattle industry have been largely due to increases in reproductive efficiency, nutritional improvements and genetic selection, however little emphasis has been placed on genetic selection for improvements of feed efficiency. Ratio-based traits that quantify feed consumed per unit of weight gain (F:G) or the inverse (G:F) are strongly associated with genetic merit for growth traits, such that favorable selection for them will result in cows with greater mature body size and greater maintenance energy requirements (Herd and Bishop, 2000; Arthur et al 2001c). Feed is the single largest variable expense associated with the production of beef, and accounts for approximately 65% of total expenses required to maintain a breeding herd (Arthur et al., 2004; Van der Westhuizen et al., 2004). Therefore, selecting for cows with lower maintenance energy requirements and improved feed utilization would greatly reduce production cost. Residual feed intake (RFI) has been shown to be moderately heritable and independent of growth and therefore may be a more appropriate for selection of breeding stock compared to ratio based traits (Herd et al., 2004; Herd and Arthur, 2009). Archer et al. (2002) and Arthur

et al. (2005) concluded that strong genetic and phenotypic relationships between intake-related traits between postweaning heifers and mature cows suggesting that selection for RFI in growing animals may be favorably associated with efficiency of feed utilization in pregnant mature cows.

Phenotypic and genetic correlations between RFI and other traits have been extensively reported, however less information is available on the relationships between post-weaning RFI and intake and efficiency of mature females. Thus, the objectives of this study were to characterize RFI in developing beef heifers and examine relationships with growth, body composition, heart rate and the subsequent intake, efficiency of forage utilization and productivity of mid-gestation females.

Materials and Methods

Experimental Animals and Design

All procedures were approved by the Institutional Animal Care and Use Committee of Texas A&M University, prior to the initiation of each trial. Performance and feed intake was measured in 43 7/8 and 72 purebred Bonsmara heifers during 2 consecutive yr (n = 62 in year 1 and n = 53 in year 2) at the O.D. Butler Jr. Animal Science Complex in College Station, TX. Heifers originated from the Texas Agrilife Research and Extension Center, in Uvalde Texas. Bonsmara is a tropically adapted *Bos taurus* breed, composed of a 62:19:19 ratio of Africaner, Hereford and Shorthorn, respectively (Corbet et al., 2006). Heifers (initial BW = 292.0 ± 36.7 kg; age = 280.3 ± 19.8 d) were stratified by BW, randomly assigned to pens (6 heifers per pen) equipped

with 6 Calan-gate feeders (American Calan, Northwood, NH) and adapted to a roughage diet for 28 d. During the 70-d studies, heifers were fed ad libitum twice daily a diet (1.99 Mcal ME/kg DM and 13% CP DM, Table 3.1) composed of 50% alfalfa chopped hay and pellets, 21.5% cottonseed hulls, and 28.5% concentrate feeds. Body weights and orts were collected at 7-d intervals for 70 d.

At the end of each postweaning trial, heifers were ranked by RFI and those with the lowest (n = 12 per yr) and highest (n = 12 per yr) RFI bred by natural service at the Texas Agrilife Research and Extension Center (Uvalde, TX). Females from yr 1 were re-bred during the same breeding season as heifers from yr 2. Following rectal palpation to determine pregnancy status, 23 1st-parity pregnant heifers and 19 2nd-parity pregnant cows were identified for use in the subsequent study, and transported to the Beef Cattle Systems Research Center (College Station, TX). Upon arrival, females were fitted with passive, half duplex electronic identification ear tags, and assigned to 1 of 2 pens (based on age) each equipped with 4 electronic GrowSafe® feedbunks (GrowSafe® DAQ 4000E; GrowSafe® System Ltd., Airdire, AB, Cananda). The pregnant cows were adapted to the experimental diet consisting of 70% chopped sorghum and 30% chopped alfalfa (2.11 Mcal ME/kg 12% CP DM, Table 3.1) for 31 d. To minimize error in measuring hay disappearance, nylon-web curtains were fitted around the perimeter of the GrowSafe® feed bunks. A vitamin and mineral supplement was provided ad libitum in separate feeders. Forage intake and feeding behavior data were collected daily, and BW measured at 7-d intervals during a 77-d study.

Table 3.1. Summary of dietary composition for heifers during the postweaning RFI trial and for mid-gestation females during the cow intake trial

Item	Postweaning Heifers	Mid-gestation Females
Dietary composition, % (as fed)		
Chopped sorghum		70
Chopped alfalfa	35	30
Pelleted alfalfa	15	
Cottonseed hulls	21.5	
Cracked corn	19.5	
Molasses	7	
Premix[1]	2	
Pasture mineral[2]		ad libitum
Chemical composition		
DM, %	90	92
ME, Mcal/kg DM	1.99	2.11
CP, % of DM	13.0	12.3
NDF, % of DM	44.8	68.5

[1]Premix contained cracked corn, salt, vitamin E at 44,000 IU/kg of product, and a trace mineral mix which contained a minimum of 19% Zn, 7.0% Mn, 4.5% Cu, 4,000 mg/kg of Fe, 2,300 mg/kg of Se, and 500 mg/kg of Co

[2]Pasture mineral contained a minimum of 14% Ca, 7.0% P, 12% salt, 4.9% Mg, 0.1% K, 2,500 mg/kg of Cu, 3,900 mg/kg of Mn, 45 mg/kg of Se, 9,900 mg/kg of Zn, vitamin A at 440,000 IU/kg of product, vitamin D at 44,000 IU/kg of product, and vitamin E at 220 IU/kg of product

Data Collection

Hip height (HH) and real-time ultrasound measurements of 12th rib-fat thickness (BF), longissimus muscle area (LM) and intramuscular fat percentage (IMF) were obtained on days 0 and 70 of the postweaning heifer trials. Hip height and ultrasound measures of LM area, BF and rump fat thickness were also obtained on days 0 and 77 of the pregnant cow trial. Real-time ultrasound data were obtained by an Ultrasound Guidelines Council field-certified technician using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer (Corometrics Medical Systems Inc., Wallingford, CT). Ultrasound images were sent to the National Centralized Ultrasound Processing laboratory (Ames, IA) for analysis. Body condition scores were recorded on days 0 and 77 of the pregnant cow trial by 2 trained individuals (1 = emaciated and 9 = obese; Wagner et al., 1988).

Measurements of Heart Rate

Within each of the growing heifer trials, preliminary RFI was calculated using 56 d intake and BWmeasurements to identify heifers with the most divergent phenotypes. Within trial the lowest (n = 8/yr) and highest (n = 8/yr) RFI heifers were selected for heart rate measurements that were collected during 3 48-h period between d 60 and 70 of the trials. Heart rate measurements of all pregnant females were collected for 7-consecutive d on individual animals beginning on d 14 of cow feeding trial. Due to equipment availability, heart rate data were collected over 5 1-wk periods, starting d 14 and ending d 49.

Heart rate of individual animals was measured using a Polar equine® transmitter and monitor (Model S610i, Polar Electro Inc., Kempele Finland). The transmitter was attached to the thorax of the animal using a girth strap constructed from 33 cm wide elastic strips with a velcro latch. The area where each electrode of the transmitter contacted the animal was clipped of hair and Electron II conductivity gel (Pharmaceutical Innovations Inc., Newark, NJ) was applied to enhance conductivity. The negative electrode was positioned on the right side of the animal 15 cm below the midline of the back and the positive electrode was positioned on the left side parallel to the point of the elbow. Heart rate measurements (beats/min) were collected at 1 min intervals by wireless transmission from the transmitter to the coded monitor placed in a pocket on the girth strap. Data was downloaded wirelessly using the Polar Equine Software® program exported to Microsoft Excel.

Measures of Feeding Behavior

Feeding behavior traits were measured for mid-gestation females during the entire 77-d trial. A subroutine of the GrowSafe data acquisition software (DAQ; version 9.25), Process Feed Intakes (v. 7.29) was used to calculate feed intake and bunk visit (BV) data. Feeding behavior data were based on in-to-out events to the feedbunk (bunk visit frequency and duration) recorded by the GrowSafe™ system. Bunk visit event data were clustered into meal events after meal criterion, defined as the longest non-feeding interval that is still part of a meal, was determined for each animal (Bailey et al., 2011). A Gaussian-Weibull distribution model was fitted to log-transformed non-feeding interval data, and the intercept of the two distributions used to define meal criterion

(Yeates et al., 2001; Bailey et al., 2012). Meal criterion was used to compute individual animal meal data (meal frequency, meal duration, meal size).

Feed Samples

Diet ingredient samples were collected weekly throughout postweaning heifer and pregnant cow trials and samples composited for chemical analysis. Moisture analysis was conducted by drying in a forced-air oven for 48 h at 105 C (AOAC, 1995), and was used to calculate DMI from feed intake data. Chemical analysis was conducted by an independent laboratory (Cumberland Valley Analytical Services Inc., Hagerstown, MD), and the Cornell Net Carbohydrate and Protein System (Version 5.0, Cornell University, Ithaca, NY) used to calculate ME concentrations of the experimental diets (Table 3.1).

Computations and Statistics for Postweaning Heifer Trials

Growth rates of individual heifers were modeled by linear regression of 7-d BW against days test using the GLM procedure of SAS. Regression coefficients were used to determine initial and final BW, mid-test metabolic $BW^{0.75}$ (MBW), and ADG for individual heifers during the 70-d trials. Residual feed intake (RFIp) was computed as the difference between actual and expected feed intake from the residual from the linear regression of DMI on MBW and ADG. Heifers were sorted by RFI and classified as low, medium or high RFI based on ± 0.5 SD from mean RFI within trial. Performance, feed efficiency, ultrasound composition traits and heart rate were analyzed using the MIXED procedure of SAS with RFI group as a fixed effect and trial as random effect. Comparisons of least square means between RFI groups were performed using Tukey's

post hoc test. Phenotypic correlation coefficients among performance, feed efficiency and ultrasound body composition traits were generated using the CORR procedure of SAS including the partial option to account for the effect of trial.

Stepwise regression analysis was performed (PROC REG, SAS) was used to determine the order in which ultrasound carcass composition traits (initial, final and gain in BF, LM area, and IMF) should be included in the base model, which included MBW and ADG. When order was determined from the stepwise regression analysis, ultrasound composition traits were sequentially added to the base model and the change in coefficient of determination used to evaluate the importance to account for additional variation in DMI, beyond that of MWB and ADG. Residual feed intake was computed using the following model:

$$Y_{ij} = \beta_0 + \beta_1 MBW_{ij} + \beta_2 ADG_{ij} + \beta_3 T_i + \beta_x X_{ijk} + €_{ij}$$

where: Y_{ij} is the DMI of the jth heifer in the ith trial, T_i is the fixed effect of ith trial, X_{ijk} is the kth body composition trait for the jth heifer in the ith trial, β_0 is the y-intercept, β_1 is the partial regression coefficient of mid-test $BW^{0.75}$, β_2 is the partial regression coefficient of ADG; β_3 is the regression coefficient on trial, β_x is the regression coefficient on body composition trait X and € is the random uncontrolled error and error associated with fixed interactions of independent variables and trial for the jth heifer in the ith trial.

Results from the stepwise regression were used to compute RFI that adjusted for variation in ultrasound measures of body composition (RFIc).

Computations and Statistics Analysis for Pregnant Cow Trials

For pregnant cows, BW were corrected for conceptus weight by subtracting the estimated weight of the conceptus from the BW collected during the 77-d trial. The products of conception weights were estimated using the following NRC (1996) equation. Day of pregnancy was determined from actual calving dates and a fixed gestation length of 286 d (Van Graan et al., 2004):

$$\text{Concetpus (kg)} = (\text{subsequent calf birth weight kg} \times 0.01828) \times e^{((0.02 \times t) - (0.0000143 \times t^2))}$$

Where t is the number of days pregnant. Linear regression of 7-d conceptus-adjusted BW against day of the trial was performed as described above to compute initial and final conceptus-adjusted BW and ADG.

Growth rates of individual cows were modeled by linear regression of 7-d conceptus adjusted BW against day of the trial using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC) and regression coefficients used to compute conceptus-adjusted ADG, initial and final BW, and MBW. Expected DMI was calculated by linear regression of DMI on conceptus-adjusted ADG and MBW using the GLM procedure of SAS (SAS Inst. Inc.).

Phenotypic correlations were generated using the CORR procedure of SAS including the partial option to account for the effect of age and RFI group on mature cow performance, feed efficiency, body composition and feeding behavior traits. The MIXED procedure of SAS was used to examine the effect of heifer RFI classification, age and the 2-way interaction on performance, efficiency, ultrasound body composition, feeding behavior traits and heart rate.

Results and Discussion

Descriptive statistics for the 115 heifers used in the postweaning RFI trials are presented in Table 3.2. The initial age of the heifers at the start of the trials averaged 280.3 ± 19.8 d across the 2 trials. In year 1 heifers were numerically heavier at a younger age at the initiation of the feeding trial compared to year 2 (306.5 ± 20 kg at 276.1 ± 20.0 d vs. 275.0 ± 24.6 kg at 284.9 ± 18.8 d, respectively). Average daily gain for heifers was 1.26 ± 0.22 kg d^{-1} and average DMI was 9.10 ± 1.16 kg d^{-1} across the 2 trials. The SD for RFI were 0.72 and 0.68 kg/d for yr 1 and 2 and were with the range of 0.66 to 0.75 reported in previous studies (Lancaster et al. (2009).

Phenotypic Correlations for Heifer Postweaning Trial

In growing heifers, ADG and MBW accounted for 60.9% of the variation in DMI, which was slightly lower than reported in previous studies (0.66 to 0.82; Basarab et al., 2003; Arthur et al., 2003; Schenkel et al., 2004; Baker et al., 2006; Lancaster et al., 2009b; Kelly et al., 2010b). Many studies have measured RFI in growing beef cattle using a medium to high energy diet (2.40 to 2.80 Mcal/kg of DM), whereas this study used a decreased energy, high roughage diet (average of 1.99 Mcal/kg of DM).

Table 3.2. Summary statistics of performance, feed efficiency and ultrasound composition traits for growing heifers during postweaning.

Trait[1]	Year 1	SD	Year 2	SD
No. of heifers	62		53	
Initial age, d	276.1	20.0	284.9	18.8

Birth BW, kg	33.1	3.7	34.8	4.4
Weaning BW, kg	226.5	39.3	210.8	26.0
Performance traits:				
Initial BW, kg	306.5	39.2	275.0	24.6
Final BW, kg	396.7	43.1	361.4	29.6
Initial hip height, cm	116.6	5.4	120.0	4.7
Final hip height, cm	125.5	4.5	124.0	5.0
ADG, kg d^{-1}	1.29	0.23	1.23	0.21
Feed efficiency traits:				
DMI, kg d^{-1}	8.72	1.14	9.54	1.03
RFI, kg d^{-1}	0.00	0.72	0.00	0.68
G:F	0.148	0.02	0.130	0.02
Ultrasound composition traits:				
Initial BF, cm	0.41	0.12	0.41	0.10
Final BF, cm	0.67	0.17	0.63	0.13
Initial LM area, cm^2	49.6	6.3	45.6	4.2
Final LM area, cm^2	59.2	6.1	56.3	5.3
Initial intramuscular fat, %	2.76	0.47	2.24	0.35
Final intramuscular fat, %	3.22	0.49	2.84	0.59

[1]RFIp = residual feed intake from base model calculated using ADG and $MBW^{0.75}$; BF = 12^{th}-rib fat thickness; LM = longissimus muscle area.

Phenotypic correlations between growth, feed efficiency traits, and ultrasound carcass characteristics are presented in Table 3.3. Dry matter intake was moderately associated with ADG (0.44; $P < 0.05$) and strongly associated with BW (0.60; $P < 0.05$). Gain to feed was negatively weakly correlated (-0.26) with DMI, and as expected

strongly correlated with ADG (0.74; $P < 0.05$) and RFIp (-0.54; $P < 0.05$). Residual feed intake from the base model was strongly correlated with DMI (0.62; $P < 0.05$). Similar to this study, phenotypic correlations ranging from 0.60 to 0.72 between RFI and DMI have been reported in other studies (Arthur et al, 2001b,c; Hoque et al. 2005; and Nkrumah et al. 2007). Koots et al., (1994) conducted a meta-review of previously published data and reported that the weighted mean genetic correlations of FCR with ADG, yearling BW, and DMI were strong (-0.67, -060 and 0.71, respectively).

Residual feed intake was negatively associated with initial BF(-0.20; $P < 0.05$), but was phenotypically independent of all other ultrasound measures of carcass composition. Basarab et al. (2003) suggested that the RFI model should be adjusted for changes in the chemical composition of gain. Previous research has indicated that carcass-fat traits have accounted for an additional 2 to 4% of variation in DMI not explained by MBW and ADG (Arthur et al., 2003; Basarab et al., 2003; Kelley et al. 2010, Basarab et al., 2011). Stepwise regression analysis revealed that initial BF and final LM area accounted for additional variation in DMI ($R^2 = 0.643$ vs 0.609), while the other ultrasound body composition traits were not significant ($P > 0.15$). Lancaster et al. (2009a) also found final LM area to be a significant source of variation in the model for

Table 3.3. Phenotypic correlations among heifer postweaning performance and feed efficiency (n = 115)

Traits[1]	Initial BW	ADG	DMI	G:F	Initial BF	Final BF	Initial LMA	Final LMA	Initial IMF	Final IMF	RFIp	RFIc
Age	0.57*	-0.09	0.27*	-0.30*	0.10	0.13	0.29*	0.28*	0.03	0.06	-0.06	-0.06
Initial BW		0.09	0.60*	-0.33*	0.52*	0.45*	0.57*	0.41*	-0.05	0.13	-0.09	-0.04
ADG			0.44*	0.74*	-0.18‡	0.08	-0.01	0.31*	-0.19‡	0.04	-0.08	-0.08
DMI				-0.26*	0.06	0.28*	0.35	0.46*	-0.22‡	0.04	0.62*	0.62*
G:F					-0.21*	-0.12	-0.26*	-0.04	-0.04	0.01	-0.54*	-0.53*
Inital BF						0.61*	0.37*	0.74*	0.22*	0.23*	-0.20*	-0.01
Final BF							0.34*	0.23*	0.09	0.29*	-0.02	0.08
Initial LMA								0.77*	-0.09	0.49*	0.06	-0.02
Final LMA									-0.11	0.09	0.11	-0.04
Initial IMF										0.49*	-0.11	-0.04
Final IMF											-0.14	-0.10
RFIp												0.96*

[1]BF = final 12th-rib fat; LMA = longissimus muscle area; IMF = intramuscular fat; RFIp = residual feed intake from base model; RFIc = carcass-adjusted RFI (initial 12th-rib fat thickness and final longissimus muscle)

*Correlations that are different from zero at $P < 0.05$

‡Correlations that are different from zero at $P < 0.10$

expected DMI in growing Brangus heifers; however the increase in R^2 from the inclusion of the trait was minimal. In a study with growing Angus bulls fed a corn silage-based diet, Lancaster et al. (2009b) found that including gain in LM area in the RFIc model did not explain additional variation in DMI, however the trait was weakly correlated with RFI, and was included in the final regression model used to compute RFIc. Conversely, several studies have reported no relationship between RFI and LM development (Kelly et al., 2010b; Shaffer et al., 2011; Nkrumah et al., 2004; Basarab et al., 2003; Arthur et al. 2001c).

Pearson (0.96) and Spearman rank (0.94) correlation coefficients between RFIp and RIFc were strong ($P < 0.05$). Other studies have reported rank correlations ranging from 0.87 to 0.95 (Basarab et al., 2003; Lancaster et al., 2005; Lancaster et al., 2009b; Durunna et al., 2011) between RFI calculated from base models of ADG and MBW and carcass adjusted models. As expected, RFI from the body composition adjusted model was phenotypically independent of all measures of ultrasound body composition; however had the same association with DMI (0.62; $P < 0.05$) as RFI from the base model. Additionally, RFIc was independent from BW, ADG, but strongly associated with G:F (-0.53; $P < 0.05$), in the same manner as RFIp. The results of this study and others indicate that adjusting RFI for body composition will allow for the selection of feed efficient cattle without affecting rate and composition of gain (Basarab et al., 2003; Lancaster et al., 2005; Lancaster et al., 2009b; Durunna et al., 2011)

Effects of RFI Class in Growing Heifers

Effects of RFI classification on performance, feed efficiency, and ultrasound body composition traits of growing Bonsmara heifers with divergent RFI are presented in Table 3.4. Of the 48 heifers selected for the subsequent pregnant female trial, heifers with low RFI tended ($P = 0.07$) to be younger at the start of the trial compared to heifers with high RFI. Heifers with divergent RFI had similar birth BW, however heifers with low RFI were heavier ($P < 0.05$) at weaning compared to heifers with high-RFI (241 vs 221 kg, respectively). Heifers classified as efficient (low RFI) consumed 20% less feed and had 19% greater G:F while maintaining similar BW, HH, and ADG. Similarly, other studies have reported that growing calves with low RFI consumed 15 – 21% less feed compared to high calves with high RFI (Herd and Bishop, 2000; Arthur et al., 2001a,b; Nkrumah et al., 2007; Lancaster et al., 2009b)

Initial IMF and BF tended ($P < 0.10$) to be greater in heifers classified as low RFI (2.63 vs. 2.39% and 0.46 vs. 0.39 cm, respectively), but were similar among the divergent RFI groups at the conclusion of the feeding trial. At the beginning of the postweaning feeding trial, LM area was similar between heifers with divergent RFI. However, heifers with high RFI had greater ($P < 0.05$) LM area compared to heifers with low RFI (59.3 vs. 55.6 cm^2, respectively) at the end of the feeding trial.

Numerous studies have reported that an increase in RFI is associated with body fatness such that low-RFI steers and heifers produce leaner carcasses (Herd and Bishop, 2000; Richardson et al., 2001; Basarab et al., 2003; Nkrumah et al, 2004; Lancaster et

Table 3.4 . Effects of residual feed intake (RFI; from base model) classification on performance, feed efficiency, and ultrasound composition traits of growing heifers selected for pregnant cow intake trial

Trait[1]	Low RFI	High RFI	SE	*P*-value
No. of heifers	24	24		
Initial age, d	278	288	3.80	0.0708
Birth BW wt, kg	34.2	34.1	1.32	0.9428
Weaning wt, kg	241	221	6.61	0.0364
Performance traits:				
Initial BW, kg	291	296	6.09	0.5419
Final BW, kg	382	388	7.44	0.5411
Final hip height, cm	126	126	0.95	0.6850
ADG, kg d^{-1}	1.30	1.32	0.05	0.8161
DMI, kg d^{-1}	8.29	10.3	0.17	0.0001
Feed efficiency traits:				
RFIp, kg d^{-1}	-0.97	0.89	0.08	0.0001
RFIc, kg d^{-1}	-0.88	0.95	0.10	0.0001
G:F, kg	0.157	0.128	0.001	0.0001
Ultrasound composition traits:				
Initial BF, cm	0.46	0.39	0.02	0.0589
Final BF, cm	0.66	0.63	0.03	0.5108
Initial LM area, cm^2	46.8	48.3	0.95	0.2765
Final LM area, cm^2	55.6	59.3	1.04	0.0124
Initial intramuscular fat, %	2.63	2.39	0.09	0.0732
Final intramuscular fat, %	3.10	3.02	0.12	0.6359

[1]RFIp = residual feed intake from base model; RFIc = carcass adjusted RFI (initial 12^{th}-rib backfat thickness and final longissimus muscle area); LM = longissimus muscle area

al., 2009a; Kelly et al., 2010a,b; Shaffer et al., 2011; Donoghue et al., 2011). Lancaster et al. (2009a) found that RFI was positively correlated with gain in BF thickness in growing Brangus heifers consuming a forage-based diet. Likewise, Shaffer et al. (2011) reported positive phenotypic correlations (0.27) between RFI in growing beef heifers and ultrasound BF, such that heifers with high RFI had greater subcutaneous fat depth. Body fatness is associated with reproductive efficiency (DeRouen et al., 1994), therefore it has been suggested that RFI of females may also be related to reproductive performance. Several studies have reported negative associations between RFI and age of puberty of growing females (Arthur et al., 2005; Basarab et al., 2007; Shaffer et al., 2011; Basarab et al., 2011).

Lancaster et al. (2009a) reported that growing Brangus heifers with low RFI had larger LM area at the start of the trial compared to their high-RFI counterparts, but the divergent groups had similar final LM area and gain in LM area. Kelly et al. (2010b) reported greater loin development in high-RFI heifers compared to low-RFI heifers fed a concentrate diet. Basarab et al. (2003) found that while RFI was not related to gain in LM area, the proportions of lean tissue in the carcass and empty body protein were negatively associated with RFI (-0.21 and -0.14, respectively).

Effect of Age on Performance, Forage Intake, Body Composition and Feeding Behavior

Five females (4 2nd-parity cows and 1 1st-parity heifer) were excluded from the study because they were non-pregnant, and 1 pregnant cow was removed from the study due to an injury. Age of 1st-parity heifers and 2nd parity cows were 20.1 and 32.1 mo, respectively at the initiation of the trial (Table 3.5). Days pregnant at the start of the trial

were similar between age groups and averaged 155.4 ± 21.0 d pregnant. Body weight, ADG, and initial HH was greater ($P < 0.05$) for 2nd-parity cows compared to 1st-parity heifers. Body condition scores were higher at the start of the trail for 1st-parity heifers (5.24 vs 4.96). Dry matter intake and cow RFI was similar between age groups. As expected, calves born to first parity heifers had were lighter at birth ($P < 0.05$) compared to calves born to 2nd-parity cows (29.9 vs. 34.0 kg, respectively), due to higher nutritional requirements for growth for heifers which can limit nutrient availability for placental and fetal growth (Holland and Odde, 1992; Greenwood and Cafe, 2007).

Effects of age and postweaning heifer RFI classification on feeding behavior in pregnant Bonsmara females are presented in Table 3.6. First-parity heifers had a greater daily frequency of bunk visits (143 vs. 93 events/d, respectively) and more bunk visits per meal (11.8 vs. 7.9 visits/meal, respectively) compared to 2nd-parity cows, however all other feeding behavior traits were similar among female age groups.

Effect of Heifer RFI Classification on Performance, Forage Intake, Body Composition and Feeding Behavior

Pregnant females classified as having low RFI as heifers consumed 22.5% less ($P < 0.05$) forage compared to their high-RFI counterparts, even though conceptus-adjusted BW and ADG were similar (Table 3.5). Basarab et al. (2007) found that cows that produced progeny with low RFI (tested on a high grain diet) consumed 12% less forage compared to cows that produced high-RFI progeny. Meyer et al (2008) used weekly rising plate meter readings and forage harvests to estimate DMI for cows identified as

Table 3.5. Effects of age and RFI classification on performance, forage intake and ultrasound measures of body composition in mid-gestation females

Trait[1]	Age		Heifer RFI class					
	1st-parity heifers	2nd-parity cows	Low RFI	High RFI	SE	Age P-value	RFI P-value	RFI x Age P-value
No. females	23	19	20	22				
Initial age, mo	20.1	32.1	25.9	26.3	0.14	0.0001	0.0532	0.8737
Days pregnant	151	160	153	158	7.80	0.1724	0.4437	0.3138
Age at calving, d	24.6	36.3	30.3	30.6	0.22	0.0001	0.4505	0.5003
Subsequent calf birth BW, kg	29.9	34.0	31.0	32.8	1.18	0.0084	0.2384	0.0372
Performance traits:								
Initial BW, kg	474	505	494	485	8.48	0.0105	0.4431	0.5697
Final BW, kg	510	552	530	531	10.2	0.0036	0.9348	0.7085
ADG, kg d^{-1}	0.47	0.66	0.51	0.62	0.05	0.0132	0.1459	0.5613
Initial BCS	5.24	4.96	5.10	5.10	0.10	0.0453	0.9985	0.8677
Final BCS	4.99	4.96	4.93	5.01	0.08	0.7425	0.4190	0.3143
Initial hip height, cm	129	132	131	131	1.05	0.0161	0.9396	0.3565
Final hip height, cm	129	132	130	131	1.23	0.1188	0.3976	0.3362
DMI, kg/d	10.3	10.3	9.00	11.6	0.55	0.9265	0.0012	0.7183
Feed Efficiency traits:								
RFI, kg d^{-1}	-0.05	-0.06	-1.16	1.06	0.42	0.9929	0.0004	0.8559
Body composition traits:								
Initial rump fat, cm	1.15	1.04	1.15	1.05	0.07	0.3033	0.3000	0.5686
Final rump fat, cm	1.13	1.17	1.18	1.13	0.09	0.7397	0.6852	0.6209
Initial BF, cm	0.84	0.74	0.80	0.78	0.05	0.1703	0.8140	0.9916
Final BF, cm	0.84	0.85	0.83	0.87	0.06	0.8980	0.6094	0.6693
Initial LM area, cm^2	65.9	65.6	63.6	67.8	1.51	0.8707	0.0475	0.6488
Final LM area, cm^2	66.3	68.9	66.3	68.9	1.62	0.2429	0.2335	0.2605

[1]Initial age = age at start of feeding trial; BCS = body condition score; RFI = phenotypic residual feed intake; LM = longissimus muscle area

Table 3.6 . Effects of age and RFI classification on feeding behavior and heart rate in mid-gestation females

Trait[1]	Age		Heifer RFI classification					
	1st-parity heifers	2nd-parity cows	Low RFI	High RFI	SE	Age *P*-value	RFI *P*-value	RFI x Age *P*-value
No. females	23	19	20	22	-	-	-	
Feeding behavior traits								
Bunk visit frequency, event d^{-1}	141.8	92.7	115.5	118.9	7.17	0.0001	0.7288	0.5177
Bunk visit duration, min d^{-1}	163.4	184.4	149.4	198.4	12.94	0.2376	0.0080	0.8752
Intake per bunk visit, g	102.5	172.5	122.4	152.6	13.92	0.0007	0.1171	0.5802
Meal criterion, min d^{-1}	13.2	15.2	15.9	12.5	1.59	0.3384	0.1173	0.1231
Meal frequency, events d^{-1}	13.0	12.2	13.2	11.9	1.0	0.5850	0.3381	0.1635
Meal duration, min d^{-1}	362.2	332.7	335.3	359.6	13.43	0.1129	0.1878	0.3529
Bunk visits per meal	11.8	7.9	9.3	10.5	0.80	0.0008	0.2573	0.1951
Intake per meal, g	1,221.8	1,252.1	1,108.1[x]	1,365.9	93.7	0.8125	0.0489	0.1244
Eating rate, g/min	28.9	31.5	27.4	33.0	1.80	0.2962	0.0277	0.4308
Heart rate, beats min^{-1}	71.0	65.9	65.8	71.1	1.74	0.0383	0.0296	0.2988

[1]Meal data calculated from meal criterion calculated from individual data and applying a Gaussian-Weibull bimodal model

high or low RFI as heifers while grazing pasture and reported 21% numerically lower intakes for efficient cows compared to inefficient cows with no impact gain or BCS.

Ultrasound measures of rump fat, BF and BCS were similar between pregnant females classified as having divergent RFI as heifers. These results agree with Herd et al. (1998) who found no differences in ultrasound measurements of rib and rump fat depth between grazing cows classified as having divergent RFI as heifers. Additionally, Lawrence et al. (2011) and Myer et al. (2008) reported no differences between in BCS, measures of ultrasound fat thickness and fat accretion in pregnant females of divergent RFI groups. Conversely, Arthur et al. (2005) reported that Angus cows selected for high RFI for 1.5 generations had greater rib and BF compared to cows selected for low RFI. However, these differences were only significant at the beginning of the breeding season. In contrast to results of Arthur et al. (2005), Basarab et al. (2007) reported that dams that produced progeny with low RFI had greater BF throughout their production cycle and loss less BW during early lactation compared to dams that produced high-RFI progeny and suggested that lower maintenance requirements of low-RFI animals may have resulted in the accumulation of more body fat. The LM area at the start of the trial was greater for females classified as high RFI as heifers compared to their low-RFI counterparts (67.8 vs 63.6 cm^2, respectively). End of test LM area was similar between pregnant females from divergent RFI groups in this study. These results are in agreement with Lawrence et al. (2011 who reported negative associations of ultrasound measures of muscle depth and RFI (-0.45) in mid-gestation beef heifers. Previous studies have reported positive correlations between body fat traits and RFI in growing animals which

may have potential unfavorable impacts on fertility of beef cattle (Basarab et al., 2003; Richardson and Herd, 2004; Lancaster et al., 2009a,b; Kelly et al., 2010). However data from this study indicates that selection for RFI postweaning will have little impact on body composition later in life.

Days pregnant at the initiation of the test and age at subsequent calving was similar among the divergent RFI groups (Table 3.5). The results of this study indicate that no differences existed between age of first conception and postweaning RFI group, however the limited number of animals examined in this study over a single production cycle is cause for caution when extrapolating the results. Arthur et al. (2005) reported a tendency for low-RFI cows to calve 5-6 d later compared to high-RFI cows. While the effect was a delay in first calving of only 5-6 d, the effect may be amplified if multiple generations of selection were applied. Several studies since have examined the effects of RFI on age at puberty, age at conception, and productivity in heifers (Shaffer et al., 2011; Basarab et al., 2011; Donoghue et al., 2011). Shaffer et al. (2011) reported a negative linear relationship between RFI and age at puberty such that a 1-unit increase in RFI corresponded to a decrease of 7.5 d in age at puberty. Finally, a recent study by Basarab et al. (2011) reported that growing heifer calves with divergent RFI reached puberty at the same age and at the same BW. However, when RFI was adjusted for final ultrasound BF and feeding event frequency, low RFI heifers reached puberty 13 d later and were 14.5 kg heavier than their high RFI counterparts They went on to report that low RFI heifers had lower rates of conception from d 12 to 37 of the breeding season and subsequently had fewer calves born by d 28 of the calving season, however when

RFI was adjusted for body composition and feeding behavior there were no differences in conception rates and delay in calving between the RFI groups. Therefore, Basarab et al. (2011) indicated that while heifers with low RFI adjusted for additional energy sinks reached puberty later, there was no impact on subsequent fertility traits such as conception rates and date of calving. Moreover, when heifers were grouped as pre and post-pubertal, the authors reported that the pre-pubertal heifers consumed 4.7% less feed and had 7.5% more desirable FCR compared to post-pubertal heifers, when ADG, BW, and BF was equal. Heifers that reached puberty near the start of within 30-60 d after the start of the RFI feeding test consumed more feed and had longer feeding event durations compared to later maturing heifers. They reported that selection for low RFI heifers from a group of pre- and post-pubertal heifers may result in later maturing heifers that lack the additional energy demands associated with sexual development and activity being ranked as more efficient (Basarab et al., 2011).

The heifer-RFI classification x female age interaction was significant for subsequent calf birth weight (Figure 3.1). Calves born to 1st-parity heifers classified as having low RFI were smaller than calves born to their inefficient counterparts (27.5 vs 32.4 kg, respectively), whereas, RFI classification had no effect on calf birth weight in 2nd-parity females. In general, calves born to 1st–parity females were smaller than those born to 2nd-parity females, due to higher nutritional requirements for growth for heifers which can limit nutrient availability for placental and fetal growth (Holland and Odde, 1992; Greenwood and Cafe, 2007). Additionally, nutritional restriction in a severe form may have a greater impact on birth weights of calves born to heifers compared to cows.

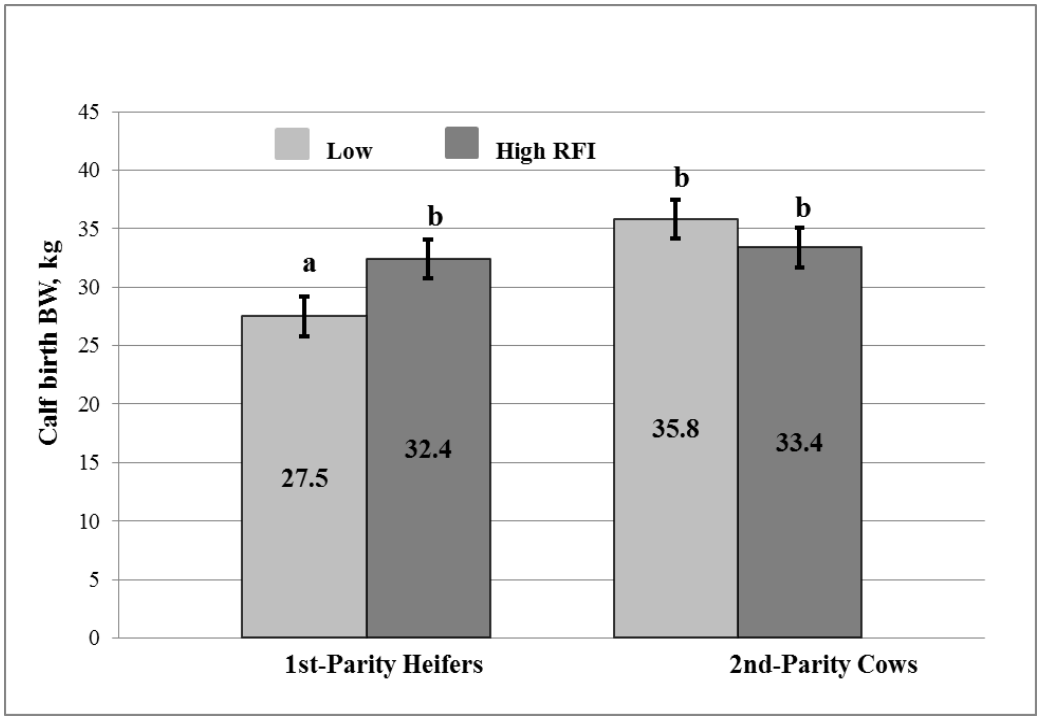

Figure 3.1. Effects of heifer RFI classification and female age on subsequent calf birth BW. Interaction of heifer RFI class and age was $P = 0.04$.

(Hennessy et al., 2002). It is possible that the lower feed intake of 1st-parity heifers classified as low RFI negatively impacted the birth weight of their calves due to additional energy requirements arising from continuing growth coupled with the requirements of placental and for fetal development. These findings are unique to this study as previous studies have found RFI classification of the cow to have no impact on calf birth weight (Arthur et al., 2005; Lawrence et al., 2011). More research is needed to fully understand the impacts of RFI classification of the dam on subsequent calf birth BW.

Daily frequency of bunk visit events was not affected by RFI group, but females classified as having low RFI as heifers spent 24.6% less time at the bunk compared to females classified as having high heifer RFI (149.4 vs 198.4 min/day, respectively) (Table 3.6). Cow RFI adjusted for conceptus was positively associated with bunk visit frequency (0.57) and bunk visit duration (0.44). In agreement, Basarab et al. (2007) reported positive associations between cow RFI adjusted for conceptus and feeding frequency (0.50) and feeding durations (0.36). While there was a tendency ($P = 0.12$) for meal criterion to be higher for females with low compared to high RFI as heifers, daily frequency and duration of meal events were similar for both RFI groups. Females with low RFI as heifers had smaller ($P < 0.05$) sized meals (1,108 vs 1,366 g), but the eating rate was greater for females with high RFI as heifers (33.0 vs. 27.4 g/min).

These results agree with studies examining feeding behavior in growing animals with divergent RFI. Nkrumah et al (2007) who found more efficient growing heifers spent 24% less time at the bunk compared to their less efficient counterparts. Moreover,

Lancaster et al. (2009b) reported that growing Brangus bulls with low RFI spent 13% less time consuming feed and had 11% fewer meals compared to their high RFI counterparts.

Results of the feeding behavior analysis indicate that females classified as having low RFI as heifers spent less time obtaining feed at the bunk, had lower intakes per meal, and a slower eating rate, all of which explain the lower DMI of the efficient females.

Cow RFI and Associations with Heifer Postweaning Traits

The variation in DMI of mid-gestation females attributed to variation in BW gain and mid-test $BW^{0.75}$ corrected for estimates of conceptus weight was 37.7%. This percentage is considerably less than previously discussed in the heifer postweaning trials (60.9%), and other studies with young growing animals, which have reported values ranging from 0.66 to 0.82 (Basarab et al., 2003; Arthur et al., 2003; Schenkel et al., 2004; Baker et al., 2006; Lancaster et al., 2009b; Kelly et al., 2010b). Lawrence reported an R^2 coefficient of 29% when correcting for conceptus-adjusted MBW and ADG in mid-gestation beef heifers consuming a grass silage diet. A greater SD (2.10) in cow RFI calculated using conceptus adjusted BW and ADG was observed compared to RFI calculated during the postweaning heifer trial (SD = 0.70). Other studies conducted with pregnant females have noted SD for RFI adjusted for conceptus weight ranging from 0.72 to 3.18 to (Basarab et al. 2007; Lawrence et al. 2011). The lower coefficients of determination associated with adult vs. growing animals observed when RFI is computed for pregnant and lactating animals compared to growing animals likely

reflects difficulty associated with accurately measuring rate and composition of changes in BW, fetal growth and milk production of adult compared to growing animals. Computation of RFI resulting in the greatest explanation in variation of DMI is dependent on accurate measurements of the component traits. In this study, BW of pregnant females were adjusted based on estimates of conceptus weight.

Step-wise regression analysis was used to examine the order of inclusion of heifer RFI, pregnant female performance, body composition, and feeding behavior traits for mid-gestation Bonsmara cows (Table 3.7). Traits were included to compute an adjusted RFI model when significant at $P < 0.15$. For this study, heifer RFI, FBW adjusted for conceptus weight, initial BCS, bunk visit per meal, bunk visit frequency, and bunk visit duration accounted for 85% of the variation in DMI. Bunk visit frequency and bunk visit duration accounted for the greatest amount of explained variation in DMI (53 and 26%, respectively). In growing animals, Lancaster et al. (2009b) reported that incorporating meal frequency and duration and head down duration to a carcass-adjusted RFI model explained 35% of variation in DMI not explained by the base RFI model. In growing pigs, de Haer et al. (1993) found that 44% of the variation in feed intake not explained by ADG, MBW, and percent lean carcass was due to eating duration and bunk visit frequency. In this study, initial BCS accounted for a small proportion of variation in explained DMI (3.5%). Lawrence et al. (2011) found that including LM depth in addition to MBW and BW gain adjusted for conceptus weight increased the R^2 of the RFI model 9% units, in mid-gestation beef heifers. Basarab et al. (2007) included gain in

Table 3.7. Regression of DMI and heifer RFI, pregnant cow performance, body composition and feeding behavior traits in mid-gestation Bonsmara females (n = 42)

Trait	Partial R^2
Heifer RFI, kg d^{-1}	0.02
Final BW, adjusted for CW, kg	0.10
Initial BCS	0.03
Bunk visit per meal	0.02
Bunk visit frequency, event d^{-1}	0.22
Bunk visit duration, min d^{-1}	0.45
Model R^2	0.85

BF, end of test tail fat, and end of test BCS, and reported a final adjusted RFI model that accounted for 39.3% of the variation in beyond conceptus weight adjusted $MBW^{0.75}$ and ADG in mature cows. In studies conducted with growing animals it has been suggested that the RFI model be adjusted for the composition of gain and generally carcass-fat traits account for an additional 2 to 4% of variation in DMI not explained by MBW and ADG (Arthur et al., 2003; Basarab et al., 2003; Kelley et al. 2010, Basarab et al., 2011). The results of this study indicate that while feeding behavior traits continue to contribute to variations in DMI in older animals, body composition may become less important.

Cow RFI as computed using BW gain and mid-test $BW^{0.75}$ corrected for estimates of conceptus weight was independent of age, cow BW, ADG and ultrasound measures of body composition. Residual feed intake for pregnant females was strongly positively correlated with forage intake (0.79) and negatively associated with G:F (-0.50). These results are in agreement with Basarab et al. (2007) who reported that cow RFI adjusted for conceptus weight was unrelated to BW, ADG, however was strongly related to forage intake (0.83). Lawrence et al. (2011) reported an even higher correlation between RFI adjusted for conceptus in pregnant beef heifers and DMI (0.85), but found no associations of RFI with BW and ADG.

Phenotypic correlations among postweaning heifer and cow traits are presented in Table 3.8. Body weight and DMI measured in growing heifers was correlated with BW and forage intake of pregnant females (0.69 and 0.54, respectively). Archer et al. (2002) reported a slightly lower phenotypic correlation between intakes of heifers

Table 3.8. Phenotypic correlations between heifer postweaning performance and feed efficiency and performance and forage intake in mid-gestation cows

	Postweaning traits				
Cow traits	Final BW	ADG	DMI	G:F	RFIp
Final BW	0.69*	0.43*	0.40*	0.17	-0.01
ADG	0.33*	0.16	0.32*	-0.09	0.17
Forage DMI	0.37*	0.21	0.54*	-0.20	0.40*
G:F	0.15	0.05	-0.05	0.08	-0.15
$RFIp_{cow}$	0.08	0.08	0.41*	-0.24	0.49*

*Correlations differed from zero at $P < 0.05$

measured during a postweaning trial and intake of mature cows (0.51). In their study, the same pelleted ration was fed to both the growing heifers and mature cows, and the mature cows were open. Gain to feed ratio measured in heifers was not correlated with G:F, and was weakly correlated (-0.20) with DMI measured during mid-gestation, suggesting that postweaning G:F has little association with subsequent efficiency of forage utilization in pregnant cows. A stronger phenotypic relationship (0.49) between postweaning heifer RFI and cow RFI was found, compared to Archer et al. (2002) who reported correlations of 0.40. Niewhof et al. (1992) reported a genetic correlation of 0.51 among RFI of dairy heifers measured postweaning and first lactation. These results, along with those previously reported indicate the females which are identified as efficient as heifers will consume less feed as cows, with little impacts on BW and ADG (Arthur et al., 1999; Archer et al et al., 2002).

Heart Rate of Heifers and Cows

Three heifers from each year were not included in analysis for heart rate due to insufficient days of complete data (less than 6 days collected). Heifers removed included 1 high and 2 low-RFI heifers from year 1 and 2 high and 1 low-RFI heifer from year 2. Heifers identified as having low RFI consumed 21% less feed, had 15% greater G:F ratios compared to heifers identified as having high RFI, while maintaining similar BW and ADG. Heifers in year 1 had significantly ($P < 0.05$) lower heart rates (82.8 beats/min) compared to heifers in year 2 (91.7 beats/min). Heifers measured in year 2 consumed 10% more feed ($P < 0.01$; data not shown) compared to heifers in year 1. The greater heart rates found in heifers from year 2 may be a result of greater feed intake.

Heart rates were similar among heifers in divergent RFI groups; these results are unexpected as heart rate has been shown to be highly correlated with energy expenditure in cattle (Yasamtoto et al., 1979; Brosh et al. 1998). These results would imply similar heat production between RFI phenotypes. Greater energy expenditures have been reported in steers with high RFI compared to those with low RFI when consuming a concentrate diet at 2.5 times maintenance requirements (Nkrumah et al., 2006).

A total of 7 females were not included the heart rate analysis due to equipment malfunctions and an inadequate number of days of measured heart rate. Heart rates of 1st-parity heifers were greater than that of 2nd-parity cows (71.0 vs 65.9 beats/min, respectively; Table 3.6) and a negative correlation between heart rate and age was observed (-0.34; $P < 0.10$). Average heart rates in this study are similar to those reported by Brosh (2007) for pregnant cows. Heat production as measured per unit of BW has been found to decrease with increasing age in heifers (Ritzman and Colovos, 1943; Freetly et al., 2003). Some factors that may contribute to the decrease in heat production per unit BW with ageing may be a decrease in the proportion of metabolically active tissues to total BW or a decrease in the rate of substrate cycles like protein turnover (Moulton et al., 1922; Lobley et al., 1980). In this study, the 2nd-parity cows were 43 kg heavier (at the end of the feeding trial) compared to 1st-parity heifers, however the age groups had similar DMI. While feed consumed per kg of BW was not significantly different between the age groups, numerically 1st-calf heifers consumed 6% more feed per unit of BW compared to 2nd parity cows, which may help explain lower heart rates of the older animals. Rezakhani et al. (2004) examined heart rates on a large group of dairy

cows and heifers of varying ages and found significant differences in heart rate between animals ages 1 to 3 years old compared to cows more than 6 years old (84.8 vs 80.1 beats/min, respectively), indicating a lower heart rates in older cows. Freetly et al. (2002) noted the necessity of accounting for both age and breed when examining the metabolic rate of sheep. Additionally, first-parity heifers have additional energy requirements due to their own continuing growth as well as that of the fetus (Holland and Odde, 1992; Greenwood and Cafe, 2007).

Heart rates for females classified as low RFI during the postweaning test were lower ($P < 0.05$) compared to females classified as having high RFI. Thus, differences in heart rate found in this study provide evidence to suggest that females with low RFI as heifers had lower heat productions compared to females with high RFI as heifers. The reasons for a lack of difference between heart rates of growing heifers with divergent RFI are unclear. Environmental conditions such as cold exposure and the metabolizable energy of the diet, as well as stress and excitement can impact heart rate (Yasamoto etal., 1979; Brosh et al., 1998; Barkai et al., 2002). While strong positive linear relationships have been found between heart rate and energy expenditure in cattle, it is still an indirect indicator (Webster, 1967; Yamamoto et al., 1979). Yasamoto et al. (1979) found that energy expenditure could be estimated within ± 10%, however only after the relationship between oxygen consumption and pulse frequency is determined for each individual animal. Therefore the results of this this study should be interpreted with caution.

Conclusions

Feed represents the largest variable cost associated with producing beef, and is a significant determinant of profitability for beef operations (Arthur et al., 2004). Growing heifers classified as efficient (low RFI) consumed 20% less feed and had 19% greater G:F, while maintaining similar BW, HH, and ADG. Subsequently, pregnant females classified as having low RFI as heifers consumed 22.5% less ($P < 0.05$) forage compared to their high-RFI counterparts, even though BW and ADG were similar. In this study, RFI classification as heifers had no subsequent effect on BW gain or body composition of pregnant females. The phenotypic relationship between RFI measured in postweaning heifers and RFI calculated in mid-gestation females found in this study (0.49) was greater than reported in previous studies (Archer et al. 2002), and indicate that growing heifers identified as efficient will maintain subsequent efficiency of forage utilization as during mid-gestation.

Females classified as having low heifer RFI spent 25% less time eating and had 7% lower heart rates compared to their high-RFI counterparts. The parity by RFI classification interaction for subsequent calf birth BW indicated that 1st-parity heifers had calves with lower birth weights compared to their high-RFI counterparts, but there was no impact on calf birth weight between RFI classification groups in 2nd-parity cows. More research is needed to fully understand the impact of RFI on birth weights in young females.

CHAPTER IV

DIET DIGESTIBILITY OF HEIFERS WITH DIVERGENT RESIDUAL FEED INTAKE AND N-ALKANE PREDICTED INTAKE OF MATURE MID-GESTATION COWS WITH DIVERGENT FEED EFFICIENCY

Introduction

Several studies have examined digestibility in beef cattle (Richardson et al, 2004; Nkrumah et al; 2006; Krueger et al., 2007, 2009; Cruz et al., 2010; McDonald et al., 2010) and sheep (Redden et al., 2010) with divergent feed efficiency, with variable results. Nkrumah et al. reported a tendency for a negative association between RFI and digestibility of dietary CP and DM such that greater DM and nutrient digestibility was associated with more efficient animals. Steers with low RFI steers were observed to have numerically greater DM digestibility (4.5 percentage units), compared to their high RFI counterparts. In agreement, McDonald et al. (2010) and Krueger et al. (2007, 2009) found negative correlations between RFI and diet DM digestibility in mature cows, growing steers and growing heifers. Richardson et al. (1996) found low RFI steers to have 1% greater DM digestibility compared to high-RFI steers, and stated that those small differences in digestibility may result in significant differences in feed efficiency. Conversely, other studies have reported no differences in digestibilities in beef cattle divergent RFI (Richardson et al., 2004; Cruz et al. 2010). Due to the conflicting reports

regarding differences in digestibility in beef cattle with divergent RFI, more research is needed to determine how digestibility impacts variations in feed efficiency.

Computation of RFI depends on accurate measurements of DMI and growth of the animal (Koch et al., 1963). Specialized feeding systems such as Calan Gate Feeders™ and the Growsafe System™ have made direct measurement of individual animal intake in confinement accurate and reliable, with little interference with animal behavior. However, intake of animals on pasture cannot be directly measured and instead must be estimated. Obtaining a reliable estimate of voluntary herbage intake in the pasture is challenging and therefore the majority of RFI research has been conducted in confinement with prepared feeds where direct measurements of individual animal intake are obtained, and the results extrapolated to grazing animals.

Alkanes have been effective to measure pasture intake and digestibility in one group of ruminants relative to another (Mann and Stewart 2003; Molina et al., 2004; Premaratne et al., 2005). It remains questionable if the methodology is accurate enough to assess variations in individual animal intake for the purpose of genetic improvement of feed efficiency (Arthur et al., 2004). The challenge still remains to refine and develop the use of alkanes to accurately provide assessments of voluntary pasture intake.

The objectives of this study were to examine the relationships between RFI and apparent diet digestibility in growing heifers and mid-gestation cows and to evaluate the use of n-Alkanes to accurately predict variations in individual-animal intake and digestibility in mid-gestation cows identified as having divergent feed efficiencies.

Materials and Methods

Animals and Experimental Design

All procedures were approved by the Institutional Animal Care and Use Committee of Texas A&M University, prior to the initiation of the trials. Performance and feed intake was measured in Bonsmara heifers over a consecutive 3-yr period (n = 62 in year 1, n = 53 in year 2, n = 60 in year 3) at the O.D. Butler Jr. Animal Science Complex in College Station, TX. Heifers originated from the Texas Agrilife Research and Extension Center, in Uvalde Texas. Bonsmara is a tropically adapted *Bos taurus* breed, composed of a 62:19:19 ratio of Africaner, Hereford and Shorthorn, respectively (Corbet et al., 2006). Heifers (initial BW = 285 ± 37.1 kg; age = 281 ± 21.4 d) were stratified by BW and randomly assigned to pens (6 heifers per pen) equipped with 6 Calan-gate feeders (American Calan, Northwood, NH) and adapted to a roughage diet for 28 d. During the 70-d studies, heifers were fed ad libitum diet twice daily (1.97 Mcal ME/kg DM and 13.5% CP DM) composed of 50% alfalfa chopped hay and pellets, 21.5% cottonseed hulls, and 28.5% concentrate feeds. Body weights and orts were measured at 7 d intervals.

At the end of each postweaning trial, heifers were ranked by RFI and those with the lowest (n = 12 per yr) and highest (n = 12 per yr) RFI bred by natural service at the Texas Agrilife Research and Extension Center (Uvalde, TX). Females from yr 1 were re-bred during the same breeding season as heifers from yr 2. Following rectal palpation to determine pregnancy status, 23 1st-parity pregnant heifers and 19 2nd-parity pregnant cows were identified for use in the subsequent study, and transported to the Beef Cattle

Systems Research Center (College Station, TX). Upon arrival, females were fitted with passive, half duplex electronic identification ear tags, and assigned to 1 of 2 pens (based on age) each equipped with 4 electronic GrowSafe™ feedbunks (GrowSafe™ DAQ 4000E; GrowSafe™ system Ltd., Airdire, AB, Cananda). The pregnant cows were adapted to the experimental diet consisting of 70% chopped sorghum and 30% chopped alfalfa (2.11 Mcal ME/kg 12% CP DM, Table 2.1) for 31 d. To minimize error in measuring hay disappearance, nylon-web curtains were fitted around the perimeter of the GrowSafe™ feed bunks. A vitamin and mineral supplement was provided ad libitum in separate feeders. Forage intake and feeding behavior data were collected daily, and BW measured at 7-d intervals during a 77-d study.

Fecal Collections

Within year, growing heifers from each postweaning trial were identified for measurements of diet digestibility based on rank for RFI for the first 56 d. Heifers with the lowest (n = 9 to 10 per yr) and highest (n = 9 to 10 per yr) RFI were identified for collection of fecal samples and feed refusals for a period of 5 d in yr 1 and 4 d in yr 2 and 3. Feces were collected twice daily at 0700 and 1800 starting on d 65 of the trials. Orts were weighed and sampled once daily during the fecal collection period and stored at -20 °C for subsequent analysis.

During the pregnant cow trial, a preliminary cow RFI was computed using data collected up to day 49 of the trial to identify 32 animals d BW and intake data was used to select 32 animals for determination of predicted intake and nutrient digestibilities using n-alkanes (C_{32}). Cow RFI were compared against values of postweaning heifer

RFI and the 32 animals whose cow RFI values remained most consistent with heifer RFI were selected. Alkane boluses were administered twice daily for 9 consecutive d. Starting on d 6 of dosing (day 56 of the trial), fecal samples were collected by rectal palpation at 0700 and 1800 daily for 5 d and immediately frozen at -20 °C. Diet ingredient samples of alfalfa and sorghum were collected daily, as were ort samples from each pen (1^{st}-parity heifers vs. 2^{nd}-parity cows) during the fecal sampling period.

N-Alkane Bolus Preparation

The alkane boluses were prepared by dissolving 20 g dotriacontane (C_{32}) in 1 L heptane. Gelatin capsules were filled approximately half full with cellulose powder and 10 mL of the C_{32} solution added to each bolus. The heptane was allowed to evaporate before the capsules were sealed. The animals were dosed with a balling gun twice daily at 0800 and 1400 to provide 400 mg of C32 daily for 9 d.

N-Alkane Analysis

All forage and fecal samples were dried in a forced-air drying oven at 60°C for 72 h and ground to 1 mm using a cyclone mill, prior to chemical analysis of digestibility and nutrient concentration and extraction and analysis for alkane via gas chromatography. Samples from morning and evening were analyzed separately for each day for each animal, to account for diurnal variation. A gas chromatography system (Agilent 6890N, Santa Clara, CA, USA) with auto sampler and Chemstation software (Agilent Technologies, Santa Clara, CS, USA) was used to determine n-alkane concentration in the feces and diet components. A weighted average of each feed ingredient was used to calculate diet C_{31} and C_{33} concentrations.

Chemical Analysis for Diet Digestibility

Daily fecal and ort samples collected from the postweaning heifer trials were composited by weight to generate a separate fecal and ort sample for each heifer. Individual feed ingredient samples were composited by weight resulting in 1 sample for each feed ingredient used in the experimental diets. A weighted average of each feed ingredient was used to calculate diet internal marker concentrations. Acid detergent insoluble ash (ADIA) was used as an internal marker to estimate digestibility coefficients.

Acid detergent insoluble ash was analyzed according to Van Soest et al. (1991) using the ADF procedure and subsequent ashing. Neutral detergent fiber and ADF were determined using an ANKOM Fiber Analyzer F200 (ANKOM Technology Corporation, Fairport, NY.) according to manufacturer's protocols. Nitrogen was determined using an Elementar Rapid N Cube (Elementar, Switzerland) and 6.25 used as a conversion factor to calculate CP (LECO Corporation, St. Joseph, MI). Mineral analysis was determined by an independent laboratory using ICP analysis of a nitric acid digest.

Calculations of Intake and Digestibility

Acid detergent insoluble ash (ADIA) was used as an internal marker to determine digestibility using the following equation:

$$\text{Digestibility (DMD), \%} = \left(1 - \frac{Ci}{Cf}\right) \times 100$$

where C_i is the concentration of the internal marker in the diet and C_f is the concentration of the internal marker in the feces. The equation was corrected for the DM concentration of the orts.

The alkane procedure as described by Dove and Mayes (1991) was used to estimate intake, using the following equation:

$$\text{Intake} = \left(\frac{Fi}{Fj}\right) Dj / \left(Hi - \frac{Fi}{Fj} Hj\right)$$

where Hi and Fi are the diet and fecal concentrations of the odd-chained alkane (C_{31} or C_{33}, respectively), Hj and Fj are the equivalent concentrations of the even-chained alkane (C_{32}) and Dj is the daily dose of the even-chain alkane.

The relative concentrations of the two endogenous alkanes (C_{31} and C_{33}) in the feed and feces were also used to determine digestibility:

$$\text{Digestibility (DMD), \%} = \left(1 - (Ri \left(\frac{Hi}{Fi}\right)\right) \times 100$$

where Hi and Fi are the diet and fecal concentrations of the odd-chained alkane (C_{31} or C_{33}, respectively) and Ri are the fecal recovery rate of the odd-chained alkane. Fecal recovery rates of 0.86 and 1.03 for C_{31} and C_{33}, respectively were obtained from a previous study with beef steers fed a mixed diet of equal parts alfalfa and fescue hay (Premaratne et al., 2005).

Simultaneous equations were used to estimate the proportion of alfalfa and sorghum consumed by individual animals:

[Alfalfa C_{31}]x + [Sorghum C_{31}]y = [Fecal C_{31}] x Fecal output

[Alfalfa C_{33}]x + [Sorghum C_{33}]y = [Fecal C_{33}] x Fecal output

where solving for x provided kg alfalfa consumed and solving for y provided kg of sorghum consumed and fecal output calculated as the dosed even alkane (C_{32}) divided by fecal concentration of C_{32}.

Computations and Statistical Analysis for Heifer Feeding Trials

Residual feed intake was calculated as the difference between actual and expected DMI from linear regression of DMI on ADG and mid-test $BW^{0.75}$ (Koch et al., 1963). Within year, heifers were ranked into three classification groups: low- RFI (< 0.5 SD), medium-RFI (± 0.5 SD), and high-RFI (>0.5 SD) of mean RFI. The mixed procedure of SAS was used to examine the fixed effect of RFI classification on nutrient performance, feed efficiency, and nutrient digestibility. The CORR procedure of SAS was used to examine phenotypic correlations between RFI, performance, feed efficiency, and nutrient digestibilities including the partial option to account for trial.

Computations and Statistics Analysis for Pregnant Cow Trials

Body weights of pregnant females recorded during the 77-d trial were corrected for conceptus weight using the following NRC (1996) equation, with day of pregnancy determined from actual calving dates and a fixed gestation length of 286 d (Van Graan et al., 2004). Conceptus-adjusted BW were determined as actual BW minus Residual feed intake (RFI) was calculated as actual minus expected DMI to meet growth and maintenance energy requirements (Koch et al., 1963). Expected DMI was calculated by linear regression of DMI on conceptus-adjusted ADG and MBW using the GLM procedure of SAS (SAS Inst. Inc.). The MIXED procedure of SAS was used to examine the effects of heifer RFI classification, age and the 2-way interaction on measured

intake, predicted intake and measurements of digestibility. (rework sentence; look at other papers)

Results and Discussion

Heifer Postweaning Trial Performance and Efficiency

Summary statistics for data collected from the 3 postweaning heifer trials are presented in Table 4.1. The initial age of the heifers at the start of the trials averaged 280 ± 21.4 d across the 3 trials. Average daily gain for heifers was 1.14 ± 0.27 kg d^{-1} and average DMI was 9.09 ± 1.33 kg d^{-1} and mean phenotypic RFI was 0.00 ± 0.93 kg d^{-1} across the 3 trials and ranged from -2.87 kg d^{-1} for the most efficient heifer to 2.99 kg d^{-1} for the least efficient heifer.

Phenotypic correlations between growth and feed efficiency traits of growing Bonsmara heifers are presented in Table 4.2. Dry matter intake of growing heifers was moderately ($P < 0.05$) associated with ADG (0.38) and highly associated with initial BW (0.58). Residual feed intake was strongly correlated with DMI (0.69) and G:F (-0.55), but was independent of BW and ADG. Effects of RFI classification on performance and feed efficiency of heifers identified for measures of diet digestibility are shown in Table 4.3. Heifers with low RFI consumed 19% less feed ($P < 0.05$) compared to heifers with high RFI and had 27% greater G:F ($P < 0.05$), while maintaining similar BW and ADG. These results are similar compared to Lancaster et al. (2009a) who reported that growing Brangus heifers with low RFI consumed 15% less feed compared to their high RFI counterparts.

Table 4.1. Summary statistics of performance and feed efficiency of growing heifers

Trait[1]	Mean	Minimum	Maximum	SD
No. of heifers	175	-	-	-
Initial age, d	280	225	315	21.4
Performance				
Initial BW, kg	285	208	391	37.1
Final BW, kg	364	265	498	45.3
ADG, kg d^{-1}	1.14	0.38	2.03	0.27
DMI, kg d^{-1}	9.09	5.78	12.8	1.33
Feed efficiency				
RFI, kg d^{-1}	0.00	-2.87	2.99	0.93
G:F	0.128	0.05	0.20	0.03

[1]Initial traits measured at d 0 of feeding trial, final traits measured on d 70 of feeding trial; RFI = residual feed intake

Table 4.2. Phenotypic correlations between heifer postweaning performance and feed efficiency (n=175).

Traits	Initial BW	ADG	DMI	G:F	RFI
Age	0.55*	-0.09	0.37*	-0.38*	0.12
Initial BW		-0.04	0.58*	-0.44*	0.01
ADG			0.38*	0.73*	-0.05
DMI				-0.33*	0.69*
G:F					-0.55*

[1]RFIp = residual feed intake

*Correlations differ from zero at $P < 0.05$

‡Correlations differ from zero at $P < 0.10$.

Digestibility of Heifers

Phenotypic correlations among heifer postweaning performance and diet digestibility are presented in Table 4.4. Residual feed intake was negatively associated with DMD (-0.46), apparent CP digestibility (-0.33) apparent NDF digestibility (-0.26) and apparent ADF digestibility (-0.26). Additionally, RFI was negatively associated with apparent Ca and P digestibility (-0.32). Dry matter intake was negatively associated with DMD (-0.28).

Estimates of diet and nutrient digestibilities in growing Bonsmara heifers as determined using acid detergent insoluble ash are presented in Table 4.5. Heifers identified as having low RFI had 3.2% greater ($P < 0.05$) DMD compared to high RFI heifers. No differences were detected between the apparent digestibilities of CP, NDF, and ADF between the divergent RFI groups. Mineral digestibility of Ca and P were also similar between the groups. The lack of differences between RFI groups in nutrient and mineral digestibilities may be due to the high standard errors. During the fecal collection period, heifers with high RFI consumed 10% more feed compared to heifers with low RFI. There was a tendency ($P = 0.11$) for heifers with low to have a higher proportion of orts relative to DMI then high-RFI heifers, reflecting lower feed intake.

Richardson et al. (1996) reported that low-RFI steers had 1% unit greater DM digestibility compared to low-RFI steers, and concluded that the small difference in DMD was equivalent to a 2.3% reduction in DMI for steers gaining 1.3 kg/d. Krueger et al. (2009) examined nutrient digestibility in growing Brangus heifers with divergent

Table 4.3. Effects of residual feed intake classification on performance and feed efficiency of growing heifers identified for measures of diet digestibility

Trait[1]	Low RFI	High RFI	SE	*P*-value
No. of heifers	29	29	-	-
Initial age, d	281.0	284.4	3.66	0.5330
Performance				
Final BW, kg	372.5	364.1	6.94	0.3926
ADG, kg d^{-1}	1.17	1.14	0.04	0.6700
DMI, kg d^{-1}	8.19	10.13	0.21	0.0001
Feed efficiency				
RFI, kg d^{-1}	-1.14	1.02	0.12	0.0001
G:F, kg	0.139	0.11	0.01	0.0001

[1]Initial traits measured at d 0 of feeding trial, final traits measured on d 70 of feeding trial; RFIp = residual feed intake

Table 4.4. Phenotypic correlations between heifer postweaning performance and diet digestibility

Traits[1]	DMD	appNDF	appADF	appCP	appCa	appP
Final BW	0.18	0.05	0.02	0.09	0.07	0.07
ADG	0.17	0.06	0.11	0.10	0.12	0.11
DMI	-0.28‡	-0.19	-0.20	-0.23	-0.23	-0.22
G:F	0.36*	0.18	0.23	0.24‡	0.26‡	0.25‡
RFI	-0.46*	-0.26‡	-0.26‡	-0.33*	-0.32*	-0.32*

[1]RFI = residual feed intake

*Correlations differ from zero at $P < 0.05$

‡Correlations that are different from zero at $P < 0.10$

Table 4.5. Dry matter intake and diet digestibility of Bonsmara heifers with divergent residual feed intake

Item[1]	Low RFI	High RFI	SE	*P*-value
No. animals	27	28	-	-
DMI, kg/d	11.7	12.9	0.28	0.0060
Orts as % DMI, kg/d	9.9	7.7	0.96	0.1067
Apparent digestibility, %				
DM	65.8	62.6	1.15	0.0488
CP	65.3	63.8	1.25	0.3862
NDF	61.6	59.8	1.38	0.2546
ADF	49.8	46.5	2.04	0.2584
Calcium	65.9	64.4	1.22	0.3914
Phosphorus	66.0	64.6	1.23	0.4061

[1]Apparent digestibility as measured using the acid detergent insoluble ash method

phenotypes for RFI while consuming a high-roughage diet. Residual feed intake was negatively correlated with DM, NDF, ADF, CP, P, Ca, Zn, and Cu digestibility and heifers with low RFI had 3% units greater DMD compared to low RFI heifers. In another study, Krueger et al. (2007) reported that RFI was moderately correlated with DMD (-0.46) in Santa Gertrudis steers fed a high-roughage diet. The results of these previous studies are consistent with this one, although the number of animals measured by Krueger et al., (2007, 2009) was greater. McDonald et al. (2010) reported a high negative correlation (-0.51) between RFI and diet DM digestibility, such that low RFI cows had greater a greater DM digestibility compared to high RFI cows (74 vs 63%, respectively).

Nkrumah et al. (2006) measured apparent digestibility of DM, CP, ADF and NDF in steers fed a high-grain diet at 2.5 times estimated maintenance requirements using the total fecal collection method. No significant differences were found between steers identified as having low, medium or high-RFI. However, a tendency for a negative association between RFI and digestibility of dietary CP (-0.34) and DM (-0.33) was reported, such that greater DM and nutrient digestibility was associated with more efficient animals. Steers with low RFI were observed to have numerically greater DM digestibility (4.5 percentage units), compared to steers with high RFI. Nkrumah et al. (2006) also noted significant differences in feeding duration between divergent RFI groups, and found them to be positively correlated to differences in fecal and methane production and negatively associated to DMD and CP digestibility, and that those associations resulted in a divergence in daily DE and ME intake between high and low

RFI steers. They tested feedlot DMI as a covariate to determine if the differences between the RFI groups were dependent on level of intake and found that the variation in DE and ME between RFI groups remained and therefore were likely independent of level of intake. In agreement, when DMI was tested as a covariate in the current study, it revealed that differences in DMD were independent of level of intake, indicating that high RFI animals may require greater intakes because of the low metabolizability of feed consumed (Nkrumah et al., 2006). Channon et al. (2004) indicated improved starch digestion was greater for steer progeny from lines selected for low residua feed intake when fed a high-concentrate feedlot diet. The differences between divergent progeny groups were still apparent even after differences in DMI were accounted for (Channon et al., 2004).

Other studies have been unable to detect differences in digestibilities in beef cattle and sheep with divergent RFI. Lawrence et al. (2011) found no relationship between digestibility and RFI in gestating heifers fed a grass-silage diet and suggested that the lack of an association may have been due to the reduced impact of feed intake on digestion from forage diets compared to studies that have evaluated concentrate diets. Richardson et al. (2004) used total fecal collections to determine DM digestibility in 16 steers with divergent RFI, but reported no differences between efficient and inefficient animals. Cruz et al. (2010) used lignin as an internal marker to calculate DM digestibility in 30 Angus x Hereford crossbred steers fed a corn based finishing ration and found no differences in DM digestibility between divergent RFI groups. However, it is important to note that a period of 60-d was used to measure the component traits of

RFI, which is less than the recommended 70 d (Archer et al., 1997), and this may have reduced accuracy for predicting individual intake and growth. Additionally, the use of lignin as a marker to measure digestibility was likely not appropriate for the corn-based diet, due to the incomplete fecal lignin recovery often seen in high concentrate diets (Van Soest 1982). Despite the lack of significance, digestibility of low-RFI steers were numerically greater by 1 and 4 % units compared to high-RFI steers (Cruz et al., 2010). Finally, Redden et al. (2010) reported no difference in digestibility among divergent RFI groups of yearling ewes previously phenotyped for RFI as growing lambs.

Selection of the type of markers used to measure diet digestibility is important especially when the goal may be to detect subtle differences between groups of animals. Acid detergent insoluble ash was used in this study, however previous studies have used lignin (Cruz et al., 2010), acid insoluble ash (AIA) (Krueger et al., 2007, 2009), and indigestible ADF (McDonald et al., 2010). In the current study, some diet ingredients proved difficult to recover using the ADIA procedure. Corn and cottonseed hulls were particularly difficult to recover, which is not unexpected as both ingredients contain very little ADIA (Bodine et al., 2002). Increased error associated with feed ingredients that are difficult to recover was a limitation of the ADIA method with this particular diet.

The results of this study indicate that heifers identified as efficient (low RFI) had 3.7% greater DMD digestibilities compared to inefficient heifers. While significant differences were not detected for the apparent digestibilities of protein, fiber and minerals, numerically greater digestion coefficients for CP, ADF, NDF, Ca, and P were present in the low RFI heifers.

Predicted Intake and Digestibility of Cows

The chemical composition and concentration of n-alkanes of the diet ingredients and orts from 1st- and 2nd-parity females is presented in Table 4.6. The endogenous n-alkane concentrations of the alfalfa were similar to previous reports (Dove and Mayes, 1996), and were substantially higher then in sorghum. Previous research indicates that some tropical forages contain insufficient C_{33} alkane for the estimate of intake by the double alkane technique. (Laredo et al., 1991). The orts for both age groups of females contained notably less C_{31} and an undetectable amount of C_{33}. The differences in alkane concentration between the orts and the diet offered is likely due to the refusals being composed largely of the stem portion of the plants, as different plant components have different alkane profiles (Dove and Mayes, 2005).

Mean predicted DMI was overestimated by 10% using C_{31}:C_{32} compared to intake measured during the 5-d fecal sampling period (9.89 vs. 8.96 ± 2.90 kg/d; Table 4.7). Dry matter intake as predicted from C_{33} gave an even greater overestimate of 16.4% compared to measured intake during the fecal sampling period (10.43 ± 2.14 vs. 8.96 ± kg/d). When compared to measured DMI from the entire 77 d feeding trial, intakes predicted from C_{31} and C_{33} provided an underestimate of 4.7% and an overestimate of 0.4%, respectively. The coefficient of determination between intake estimated by C_{31} and C_{33} and measured intake for the fecal sampling period were 0.63 and 0.61. Olivan et al. (2007) compared measured intakes of non-lactating non-pregnant mature beef cows consuming alfalfa hay at low and high levels of intake (1.1 vs 1.8 kg

Table 4.6. Chemical composition and concentration of n-alkanes of diet, diet ingredients, and orts of mid-gestation females

Item[1]	Alfalfa	Sorghum	Diet[1]	1-st Parity Heifer Orts	2nd-Parity Cow Orts
DM, %	91.7	92.5	92.3	92.4	94.7
CP, % DM	17.2	6.1	9.4	6.1	5.6
NDF, % DM	54.9	68.7	64.5	71.6	77.7
ADF, % DM	35.3	40.8	39.1	44.5	47.3
C_{31}, mg/kg DM	377	37	140.4	35	23
C_{33} mg/kg DM	31	24	26.1	0	0

[1] Nutrient composition and concentration of n-alkanes of diet calculated by the weighted average of diet ingredients

DM/100 kg BW). The coefficient of determination between actual and alkane estimated intakes were higher when alfalfa was fed at the lower level of intake (r^2 = 0.74 vs. 0.65). The greatest agreement between alkane estimated intake and measured intake was observed for animals at the low feeding level with the alkane pair C_{25}:C_{24}, where the mean intake was overestimated by 11%. Hendrickson et al. (2002) found similar regression parameters for measured and estimated values for voluntary intake of Brahman-cross steers consuming buffel-grass using the alkane pairs C_{31}:C_{32} and C_{33}:C_{32} (r^2 = 0.73 and 0.72, respectively). In these studies the variation between apparent digestibility and subsequent recovery in the feces of n-alkanes was an important limitation of the use of the method to predict individual animal intakes (Hendrickson et al., 2002; Olivan et al., 2007).

Effects of age and RFI classification on measured intake, n-alkane predicted intake, and digestibility of pregnant Bonsmara females consuming a forage diet are presented in Table 4.8. Measured forage intake was not different between the age groups during the 77-d trial or during the 5-d fecal sampling period. However, females classified as having low RFI as heifers consumed 29.6% and 31.8% less ($P < 0.05$) during the feeding trial and during the fecal collection period, respectively, compared to females classified as high RFI as heifers. Intakes predicted from alkanes indicated significant differences ($P < 0.05$) in intake between the age groups, such that 2nd-parity cows consumed more feed compared to 1st-parity heifers. Alkane predicted intake from C_{31}:C_{32} and C_{33}:C_{32} was found to be 15 and 13% less ($P < 0.05$) for females classified as low RFI as heifers compared to their high RFI counterparts. Previous research has

Table 4.7. Descriptive statistics for measured intake, alkane predicted intake, alkane predicted digestibility

Item[1]	Mean	SD	Min	Max
Measured Intake				
70-d Feeding DMI, kg d^{-1}	10.38	2.90	4.68	16.64
5-d Fecal Sampling DMI, kg d^{-1}	8.96	2.90	3.74	14.81
Alkane Predicted Intake				
C_{31} Predicted Intake, kg d^{-1}	9.89	2.21	6.91	15.52
C_{33} Predicted Intake, kg d^{-1}	10.43	2.14	7.51	16.05
Alkane Predicted Digestibility				
C_{31} Predicted DMD, %	51.5	3.5	40.0	55.9
C_{33} Predicted DMD, %	46.6	3.6	34.1	50.8

[1] DMD = dry matter digestibility; Alkane estimated digestibility calculated using alkane predicted intakes from C_{31} and C_{33}, and recovery values of 0.868 and 1.03, respectively

indicated that the paired n-alkane method is adequate to predict intake of cattle on pasture on a group basis (Mann and Stewart 2003; Molina et al., 2004; Premaratne et al., 2005). Mann and Stewart (2003) reported that intake of tropical forage harvested daily and measured by Calan-gate feeders was comparable to herbage intake calculated by paired alkanes (6.28 ± 0.24 vs. 6.21 ± 0.15 kg/d, respectively) in yearling bulls grazing Kikuyu pasture. A study conducted with Angus steers compared n-alkane estimated intake of alfalfa and fescue/alfalfa mixed diets in steers to individual measurements of intake. The authors reported that average forage intake for the steers calculated from the C_{33}:C_{32} ratio was underestimated by 4.86 and 0.69% for the alfalfa and fescue/alfalfa diets respectively, but the differences between alkane predicted intakes and measured intakes were not significantly different. In agreement Molina et al. (2004) reported no difference between herbage intake measured from individually fed lactating cows and intake estimated from C_{31}:C_{32} and C_{33}:C_{32} alkanes. Discrepancies in the prediction of forage intake using alkane markers can occur due to a variety of factors. Low levels of endogenous alkane, level of intake of the animal, inconsistent release rate of dosed alkane, unequal recovery rates of alkane pairs, greater intake of concentrate compared to forage, unrepresentative sampling of diet and diurnal variation have all been described as factors that may hinder the accuracy of alkane predicted intake and digestibility (Dove and Mayes 1991;Reeves et al., 1996; Hendricksen et al., 2002; Charmley et al., 2003; Elwert et al., 2004; Ouelett et al., 2004; Premaratne et al., 2005; Smith et al., 2005; Olivan et al., 2007).

Table 4.8. Effects of age and RFI classification on n-alkane predicted intake and digestibility of mid-gestation females

Trait[1]	Age		Heifer RFI classification		SE	Age P-value	RFI P-value	RFI x Age P-value
	1st-parity heifers	2nd-parity cows	Low RFI	High RFI				
No. females	16	15	15	16	-	-	-	-
Measured Intake								
77-d Feeding DMI, kg d^{-1}	10.36	10.26	8.52	12.11	0.85	0.9075	0.0002	0.4114
5-d Fecal Sampling DMI, kg d^{-1}	8.90	8.89	7.22	10.58	0.89	0.9961	0.0008	0.5100
Alkane Predicted Intake								
C_{31} Predicted Intake, kg d^{-1}	8.91	10.85	9.07	10.69	0.47	0.0066	0.0208	0.2157
C_{33} Predicted Intake, kg d^{-1}	9.47	11.38	9.69	11.16	0.48	0.0060	0.0300	0.2252
C_{31}:C_{33} ratio	5.04 : 1	5.12 : 1	5.02 : 1	5.15 : 1	0.03	0.1204	0.0052	0.2903
Alkane Predicted Digestibility								
C_{31} Predicted DMD, %	51.7	51.2	51.5	51.3	0.95	0.6900	0.8879	0.3316
C_{33} Predicted DMD, %	47.3	45.9	47.2	45.9	0.92	0.2993	0.3725	0.3803
Proportion of alfalfa consumed	28.2	27.6	27.4	28.4	0.26	0.1718	0.0143	0.5150
DMD Adjusted for alfalfa								
DMD measured by C_{31},%	50.6	51.4	51.1	50.9	1.18	0.6106	0.8776	0.8555
DMD measured by C_{33},%	47.1	45.9	47.1	45.9	0.94	0.3648	0.3715	0.4446

[1] DMD = dry matter digestibility; Alkane estimated digestibility calculated using alkane predicted intakes from C_{31} and C_{33}, and recovery values of 0.868 and 1.03, respectively; Proportions of alfalfa consumed by individual animals estimated by simultaneous equation using C_{31} and C_{33}; DMD was adjusted using proportions of alfalfa estimated using simultaneous equation

In the current study discrepancies between measured and alkane predicted intakes may be due to low concentrations of endogenous alkanes in the sorghum portion of the diet (37 and 24 mg/kg DM for C_{31} and C_{33}, respectively). Laredo et al. (1991) noted that some tropical forages may have insufficient concentrations of C_{33} alkane for the prediction of intake using the double alkane method. Additionally, they noted that while the leaves of sorghum contained sufficient concentrations of C_{31} alkane to predict intake, the estimates may be underestimated by 5%.

The computation of RFI depends on accurate measurements of DMI and growth of the animal (Koch et al., 1963). Reliable estimates of intake are necessary for the calculation of RFI in grazing cattle and to compare intakes of cattle already identified as having divergent RFI. An Australian study used dosed alkanes contained in an intraluminal controlled-release device to estimate intake and DM digestibility in 41 lactating cows that had been previously identified as having divergent RFI as growing heifers (Herd et al. 1998). Results from this study found no differences in selectivity of plant components or DMI between high- and low-efficiency cows while grazing irrigated oat pasture. However, the authors reported discrepancies of intake estimates between the 2 pairs of alkanes used (C31:C32 and C33:C32) and attributed the error to adjustments for differences in recovery by using previously published recoveries. Another study by Herd et al. (2002) used alkanes to estimate DM digestibility and intake in 53 Angus steers grazing pasture following 1 generation of divergent selection for RFI. No differences were found between DMI and digestibility were detected between the divergent groups, however there was a tendency ($P < 0.10$) for steers with low RFI to

consume a higher proportion of rye grass and less fescue compared to their inefficient counterparts. The authors reported no evidence that the digestibility of the forage consumed differed between the RFI selection lines. In the current study, differences in forage intake between females classified as divergent RFI as heifers were detected using the paired n-alkane method, however it is important to note that the differences of measured intake between the groups were greater than found in previous studies. Females classified as having low RFI as heifers consumed 29.6% and 31.8% less ($P < 0.05$) during the feeding trial and during the fecal collection period, respectively, compared to females classified as high RFI as heifers. Arthur et al. (1999) reported that mature cows classified as having low net feed efficiency as heifers consumed 51 kg less feed during a 70 day test feeding test compared to cows classified as having high net feed efficiency. Additionally, Basarab et al. (2007) found that cows that produced progeny with low RFI (tested on a high grain diet) consumed 12% less forage compared to cows that produced high-RFI progeny. Meyer et al (2008) used weekly rising plate meter readings and forage harvests to estimate DMI for cows identified as high or low RFI as heifers while grazing pasture and reported 21% numerically lower intakes. With the extensive spread in intakes between the divergent RFI groups in the current study, the ability of the n-alkane makers to detect differences should be interpreted with caution.

When proportions of alfalfa consumed by individual animals were estimated using simultaneous equations, pregnant females classified as high RFI as heifers consumed 1% more ($P < 0.05$) alfalfa in their diet compared to females classified as low

RFI. This agrees with the observed ratios of endogenous alkanes in the feces, which indicated that pregnant cows identified as having high RFI as heifers consumed more alfalfa compared to their efficient counterparts, as indicated by a greater ratio ($P < 0.05$) of C_{31}:C_{33}. Digestibility coefficients as estimated from each endogenous alkanes were similar between the age and efficiency groups. When digestibility as measured by either endogenous alkane was adjusted for proportions of alfalfa consumed on an individual animal basis, digestibility remained similar between RFI groups. Differences in digestibility between divergent RFI groups as estimated by n-alkanes have not been previously reported. Herd et al., (1998) and Herd et al., (2002) found no differences in digestibility in lactating cows and steers grazing forage. In agreement with these grazing studies, no differences in DMD were predicted in the current study between pregnant females classified as having divergent RFI as heifers. It is possible that the ability of the alkane method to detect differences in DMD was impacted by diet selectivity.

Conclusions

Results from this study indicated that growing heifers with low RFI consumed 19% less feed compared to heifers with high RFI and, while maintaining similar BW and ADG. Heifers identified as having low RFI had 3.2% greater DM digestibility compared to high RFI heifers, however apparent digestibility of CP, NDF, ADF, Ca, and P were similar. Residual feed intake was negatively associated with DMD, CP, NDF, ADF, Ca and P digestibility.

In mid-gestation cows consuming a mixed alfalfa-sorghum diet, C_{31} gave the closest prediction of DMI compared to the intake measured during the 5 d fecal sampling period (9.89 ± 2.21 vs. 8.96 ± 2.90 kg/d), but still overestimated intake by 10%. Alkane predicted intakes successfully detected differences in level of intake between mid-gestation cows identified as having divergent RFI as heifers. These results are promising for the use of n-alkanes to identify grazing animals with divergent feed efficiencies and to monitor intake levels between groups of animals already identified as having divergent feed efficiencies. However, these results should be interpreted with caution as the spread of intake between the feed efficiency groups in this study was greater than those in previous studies.

This data indicates that cows classified as inefficient consumed a greater proportion of alfalfa compared to their efficient counterparts. Digestibility estimated by endogenous alkanes was similar among the divergent RFI groups. It is possible that the usefulness of the alkane predicted intake and digestibility in this study is being affected by the low levels of C_{33} found in the sorghum component of the diet or by differing diet selectivity of individual animals.

CHAPTER V

SUMMARY

Feed represents the largest variable cost associated with producing beef, and is a significant determinant of profitability for beef operations (Arthur et al., 2004). Results from the first study found that RFI in growing bulls was not phenotypically associated with SC or sperm motility, but was weakly associated in an unfavorable manner with sperm morphology in growing bulls. Inclusion of RFI as a component of a multi-trait selection program has the potential to improve the profitability of beef production systems with minimal effects on performance traits and bull fertility.

In the second study, growing heifers classified as efficient (low RFI) consumed 20% less feed and had 19% greater G:F, while maintaining similar BW, HH, and ADG. Subsequently, pregnant females classified as having low RFI as heifers continued to consume 22.5% less forage compared to their high-RFI counterparts, even though BW, ADG and body composition were similar. Pregnant females classified as having low RFI as heifers spent 25% less time eating and had 7% lower heart rates compared to their high-RFI counterparts. A parity by RFI classification interaction indicated that 1st-parity heifers had calves with lower birth weights compared to their high-RFI counterparts, but more research is needed to fully understand the impact of RFI on birth weights in young females. The phenotypic relationship between RFI measured in postweaning heifers and RFI calculated in mid-gestation females was moderate and indicated that growing heifers

identified as efficient will maintain subsequent efficiency of forage utilization as pregnant cows.

In the final study, growing heifers identified as having low RFI had 3.2% greater compared DM digestibility to high RFI heifers, Residual feed intake was negatively associated with DMD, CP, NDF, ADF, Ca and P digestibility. When investigating the usefulness of the n-alkane method to predict variations in individual animal intake, C_{31} gave the closest prediction of DMI compared to the intake measured during the 5 d fecal sampling period, but still overestimated intake by 10%. Alkane predicted intakes successfully detected differences in level of intake between mid-gestation cows identified as having divergent RFI as heifers. These results are promising for the use of n-alkanes to identify grazing animals with divergent feed efficiencies and to monitor intake levels between groups of animals already identified as having divergent feed efficiencies. Fecal concentrations of n-alkanes indicate that cows classified as inefficient consumed a greater proportion of alfalfa compared to their efficient counterparts. Digestibility estimated by endogenous alkanes was similar among the divergent RFI groups. It is possible that the usefulness of the alkane predicted intake and digestibility in this study was affected by the low levels of C_{33} found in the sorghum component of the diet or by differing diet selectivity of individual animals. More research using this methodology is necessary to further explore the use of n-alkanes to predict individual animal intake and examine diet selectivity in animals with divergent RFI.

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